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THE APPENDICULAR MYOLOGY OF THE LABRADOR DUCK (*CAMPTORHYNCHUS LABRADORIUS*)

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The Labrador Duck (*Camptorhynchus labradorius*, Gmelin) has been extinct for almost 100 years, the last specimen having been taken in 1878. The species occurred formerly along the east coast of North America from the Ungava Peninsula to the Delaware River and perhaps to Chesapeake Bay (Palmer 1976). Little is known about its habits or internal anatomy, and nothing is known about its myology.

The purpose of this paper is to describe the distal musculature of the wing and leg of the Labrador Duck. The unique history of a study skin of an adult male in the collections of the Smithsonian Institution (USNM 1972) gave us the opportunity to do this. About twenty years ago, Humphrey and Butsch (1958) realized that they could study the pterylosis and osteology of the Labrador Duck by temporarily dismantling a study skin of the species. On removing the limb bones, they also found that the distal musculature was "well enough preserved to warrant description." The limb bones and muscles removed from that specimen are the basis for this study. Surprisingly, no broad comparative survey of hindlimb myology of waterfowl has yet been published. Studies on a few species are those of Stolpe (1932), Miller (1937), František (1934) and Ruck (1949), and more recently, Raikow (1970) analyzed diving adaptations in the stifftail ducks. Even fewer studies of forelimb myology are available. The most complete work is still that of Fürbringer (1888), who dealt mainly with the shoulder and proximal portion of the wing. Brief descriptions of wing muscles in a few species and a detailed analysis of their functions in relation to flight were presented by Sy (1936). Lacking broadly comparative information on anatid myology we made no systematic comparison of the Labrador Duck with other species; by contrast our comparison of the cleaned limb bones with skeletons in the Smithsonian Institution and with information presented by Woolfenden (1961) provided some taxonomic clues that conclude this paper.

Only the distal half of each humerus was present and only the distal muscles remained on either humeral element. The remainder of the forelimb bones and muscles were in surprisingly good condition. As all the feathers were retained with the skin, M. expansor secundariorum could not be demonstrated. Each hindlimb included the distal half of the tibiotarsus, the tarsometatarsus, and all phalanges of all toes except the ungual phalanges, which remained with the skin. In some instances complete bellies of muscles were absent and only the tendon of insertion is described. Also, due to the extremely dehydrated condition of all muscles, the presence of several small muscles and fiber architecture even of larger ones could not always be demonstrated. Dissection was performed with a stereomicroscope and drawings were made with the aid of a camera lucida microscope attachment. We referred to one fluid specimen each of Oldsquaw (*Clangula hyemalis*) and White-winged Scoter (*Melanitta deglandi*) to clarify our interpretation of the dried muscles of *Camptorhynchus* and some points were also checked against the Common Eider (*Somateria mollissima*). Bentz wrote the initial descriptions and Zusi made the illustrations. The entire paper was reviewed and modified by both authors. One leg and one wing were skeletonized; their counterparts are retained in alcohol.

We follow the myological nomenclature of George and Berger (1966). Where their terminology differs from that being developed by the International Committee on Avian Anatomical Nomenclature, we have added the new name in parentheses. The new terms have already been employed in certain studies (Raikow 1976, 1977). We use the terms "major digit" and "minor digit" for wing digits II and III, and "major metacarpal" and "minor metacarpal" for metacarpals II and III, respectively. The term "alular phalanx" refers to the pollex. The directional terms "dorsal" and "ventral," "cranial" and "caudal" as applied to the forelimb, refer to the horizontally extended wing.

MUSCLES OF THE FORELIMB

M. biceps brachii (Not shown). This muscle inserts by two parallel tendons that pass dor-

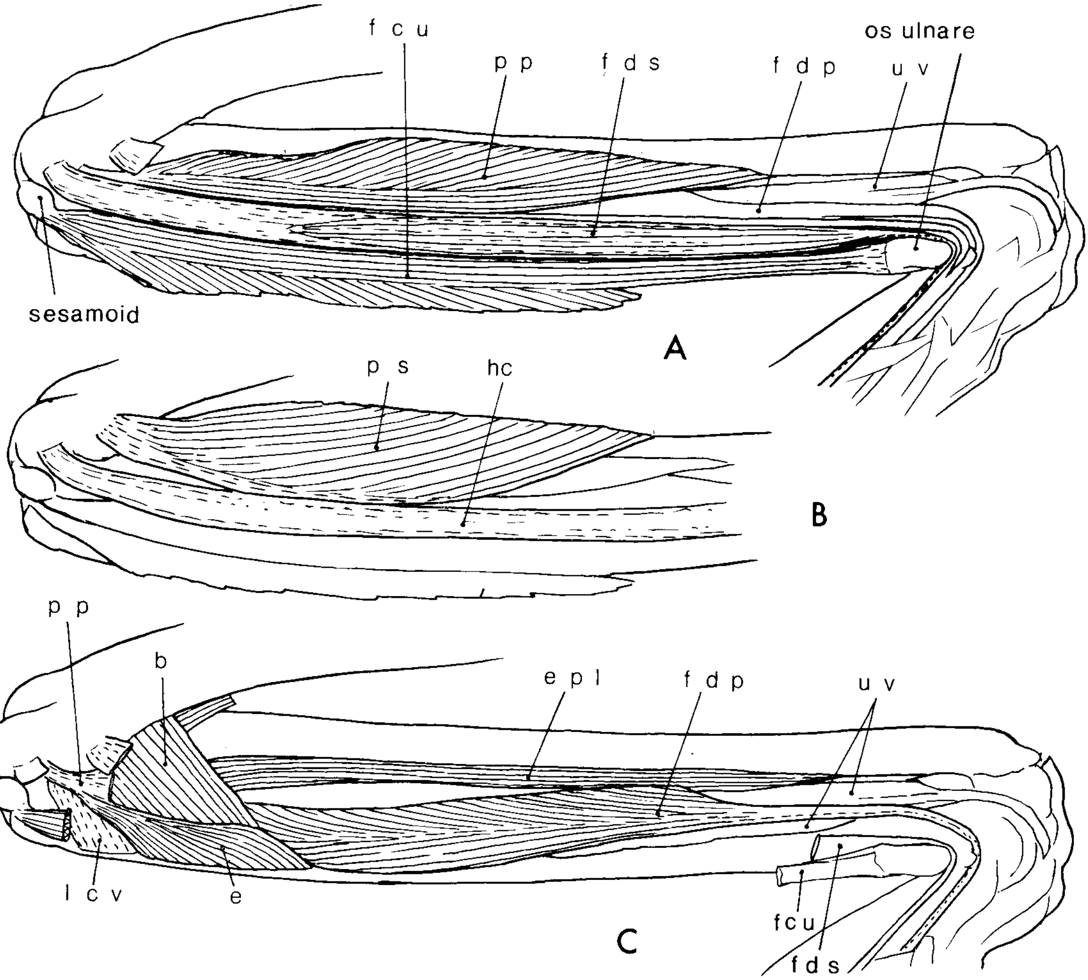

FIGURE 1. Ventral views of left forearm of *Camptorhynchus.* (A and B) Superficial muscles; M. pronator superficialis removed in A. (C) Deep muscles.

sal to M. brachialis. One inserts on the proximocranial surface of the ulna. The other inserts on the proximoventral surface of the radius and sends a branch to the distal end of the first tendon and the adjacent portion of the ulna.

M. brachialis (Fig. 1C; b). This muscle has a fleshy origin on the distal end of the humerus just proximal to the condyles. The fibers of the belly pass distally along the cranial border of the ligamentum collaterale ventrale (l c v) and insert fleshy on the ventral surface of the proximal end of the ulna. Its insertion is deep to the belly of M. entepicondyloulnaris.

M. pronator superficialis (Fig. 1B; p s). This muscle arises by a stout tendon from a shallow depression near the medial epicondyle of the humerus. The belly fans out to insert by semitendinous fibers on the cranioventral surface of at least the proximal half of the radius.

M. pronator profundus (Fig. 1A; p p). This muscle arises by a strong tendon from the medial surface of the distal end of the humerus just deep and slightly proximal to the origin of the humerocarpal band (h c). The fan-shaped belly passes distally to a fleshy insertion on the ventral surface of the proximal two-thirds of the radius.

M. flexor digitorum superficialis (Figs. 1A, 3A, 4C; f d s). This muscle arises by a short tendon from the medial condyle of the humerus and is completely ensheathed by the humerocarpal band. The spindle-shaped belly passes distally and ends on a narrow tendon that passes into the hand in a shallow groove on the cranial surface of the os ulnare. The tendon attaches to the proximal end of the first phalanx of the major digit, encloses a sesamoid, and continues distally to insert on the cranial surface of the proximal end of the second phalanx of the major digit, ventral to the insertion of M. extensor indicis longus.

M. flexor digitorum profundus (Figs. 1C,

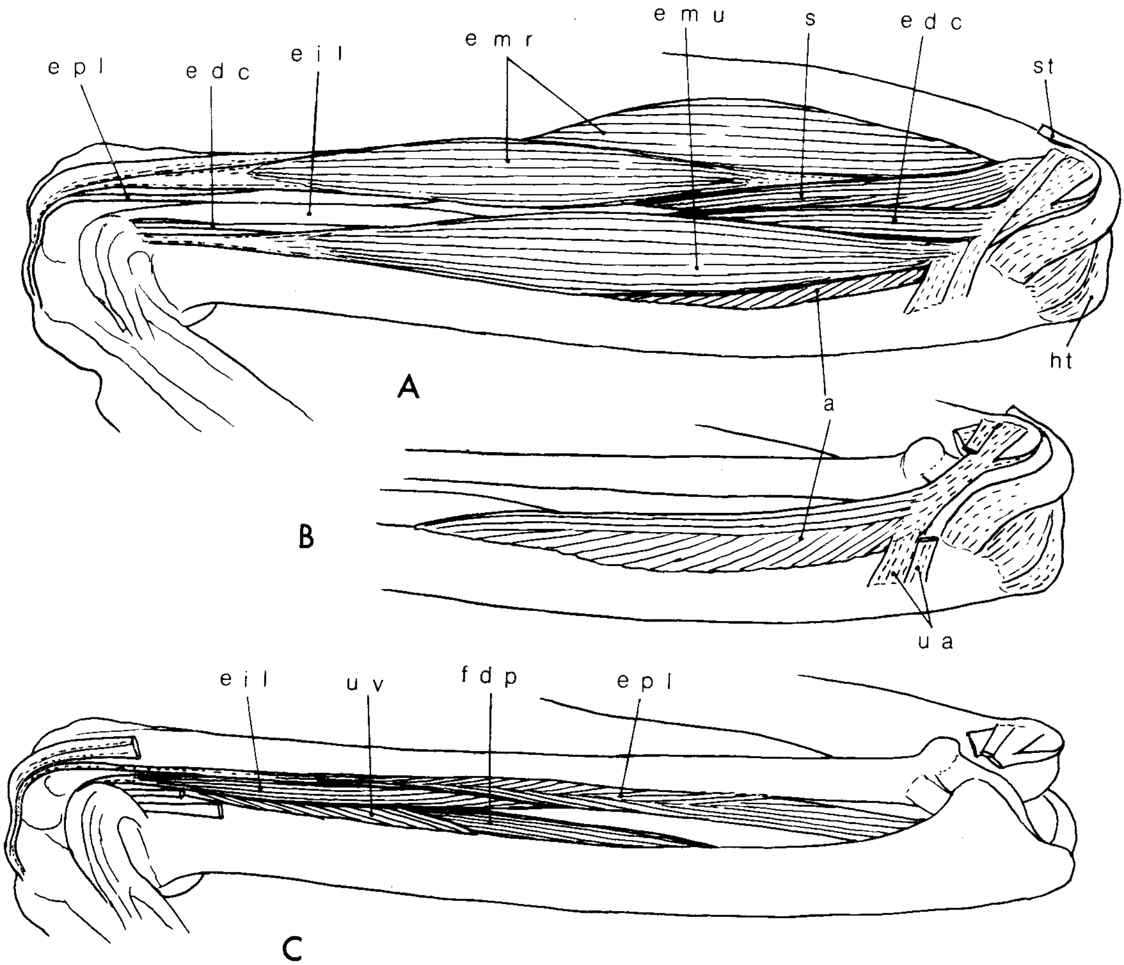

FIGURE 2. Dorsal views of left forearm of *Camptorhynchus*. (A) Superficial muscles. (B) M. extensor metacarpi ulnaris removed from its common tendon of origin with M. anconeus. (C) Deep muscles.

3A, 4C; f d p). This large muscle lies superficial to M. ulnimetacarpalis ventralis and arises by two fleshy heads from the cranioventral surface of the ulna. The belly extends most of the length of the forearm and ends on a strong tendon that passes craniad to the os ulnare, around the pisiform process of the carpometacarpus, and into the hand. The tendon passes along the cranioventral edge of the carpometacarpus where it gradually crosses the tendon of M. flexor digitorum superficialis caudally. At the distal end of the first phalanx of the major digit the tendon curves abruptly cranially and ventrally to pass through a fibrous loop (not shown) and an adjacent bony loop (not shown) on the proximocranial edge of the second phalanx. From this loop the tendon continues along the cranioventral edge of the second phalanx to insert on the proximoventral edge of the tiny third phalanx.

M. entepicondyloulnaris (Fig. 1C; e). This muscle has a common tendinous origin with M. pronator profundus from the medial epicondyle of the humerus. The belly fans out caudodistally and inserts fleshy on the ventral surface of the proximal one-fourth of the ulna, ventral and caudal to the insertion of M. brachialis. George and Berger (1966: 354) referred to this muscle as the "gallinaceous" muscle, stating that it was known only in kiwis (*Apteryx*), the Galliformes and tinamous. It is clearly present in *Camptorhynchus* and we found it also in the other ducks we examined.

M. flexor carpi ulnaris (Fig. 1A; f c u). This is the most caudal muscle on the ventral side of the wing. It arises by a strong tendon from the distal end of the medial condyle of the humerus, passes caudal and lateral to a large sesamoid and gives rise to a strong, tendinous belly. The sesamoid is anchored by ligaments to the medial condyle of the humerus and to the olecranon process of the ulna. The

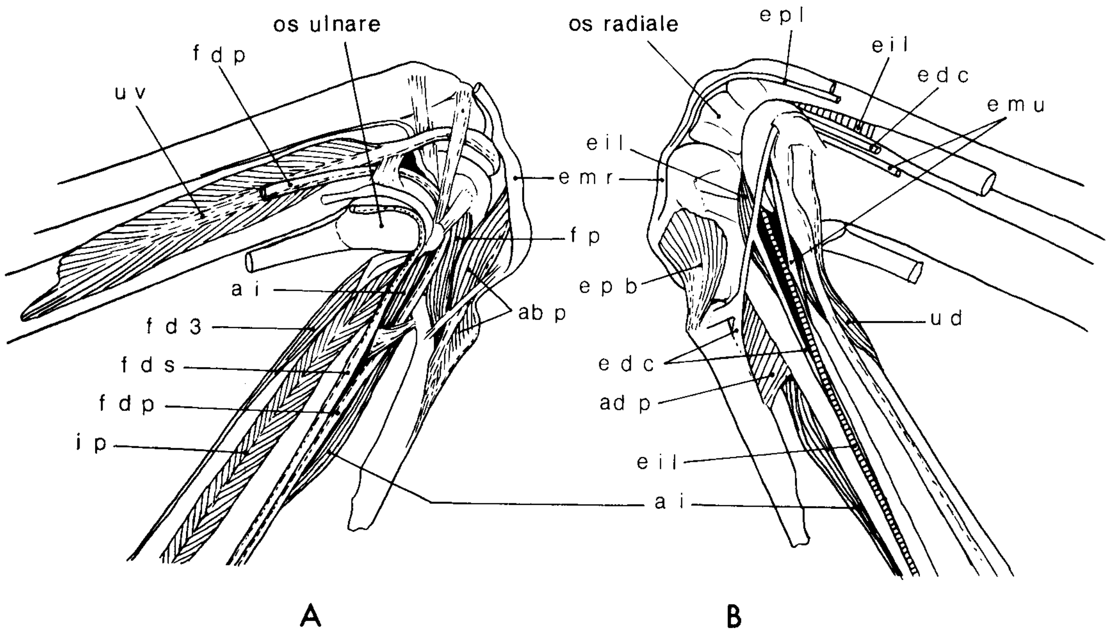

FIGURE 3. Muscles of the wrist and manus of the left wing of *Camptorhynchus*. (A) Ventral view. (B) Dorsal view. Tendon of M. extensor indicis longus crosshatched for clarity.

tendon of origin extends distally through the center of the circumpennate belly, sending fibers to the superficial ensheathing aponeurosis that becomes the tendon of insertion. The superficial aponeurosis is developed most strongly along the cranial edge of the belly. The 45 mm-long belly extends three-fourths the length of the forearm and ends on a strong tendon that inserts on the proximal surface of the os ulnare. Additional fibers attached along the caudal surface of the main belly but their connections to secondary feathers were not present.

M. ulnimetacarpalis ventralis (*M. ulnometacarpalis ventralis*) (Figs. 1C, 3A; u v). The bipennate belly of this muscle has a fleshy origin on the ventral surface of the distal half of the ulna. The short, strong tendon of insertion passes deep to a ligamentous band and inserts on the craniodorsal surface of the carpometacarpus proximal to the level of the extensor process.

M. triceps brachii (*M. humerotriceps* plus *M. scapulotriceps*) (Fig. 2A; ht, st). As in other birds, this muscle is composed of two parts. Only the distal 10 mm of the tendon of insertion of M. humerotriceps remained on the specimen. The tendon passes between the lateral and medial condyles of the humerus, ventral to a large sesamoid, the patella ulnaris, and inserts in a shallow depression on the olecranon process of the ulna. M. scapulotriceps was also represented only by its tendon of insertion. This tendon encloses the patella ulnaris just before it inserts on the coronoid process of the ulna. A thin sheet of tendinous fibers connects the two tendons of insertion and attaches on the ulna between them.

M. extensor metacarpi radialis (Figs. 2A, 3A, B; e m r). This large muscle consists of two parts. The main part arises by both fleshy and tendinous fibers from the lateral aspect of the distal end of the humerus just proximal to the origin of M. supinator. The belly extends most of the length of the forearm and ends on a strong tendon that inserts on the extensor process of the carpometacarpus. The second part begins as a tendon that arises from the proximal portion of the caudal edge of the main tendon. This separate tendon passes distally and gives rise to a spindle-shaped belly. The latter ends on a narrow tendon that rejoins the main tendon prior to its insertion on the carpometacarpus.

M. extensor metacarpi ulnaris (Figs. 2A, 3B; e m u). This muscle has its origin by two separate tendons. The larger of these arises from the lateral surface of the ectepicondyle of the humerus, while the smaller arises from from the distal edge of the ectepicondyle. These tendons shortly fuse to form a common tendon of origin for both M. extensor metacarpi ulnaris and M. anconeus. A small tendinous ulnar anchor (u a) arises from this common tendon of origin; it passes caudally and inserts on the ulna distal to the ulnar anchor of M. extensor digitorum communis. M. extensor metacarpi ulnaris arises from the distalmost portion of the common tendon at about the distal limit of the ulnar anchor. The large belly extends three-fourths the length of the ulna and ends on a tendon that passes deep to a ligamentous loop at the distal end of the ulna. The tendon inserts on the caudodorsal edge of the proximal end of the shaft of the major metacarpal.

M. anconeus (*M. ectepicondylo-ulnaris*) (Figs. 2A, B; a). This fan-shaped muscle arises from the ventral surface of the proximal portion of the common tendon of origin for this muscle and M. extensor metacarpi ulnaris. The muscle extends distally and inserts fleshy on all but the distal few millimeters of the proximal two-thirds of the craniodorsal surface of the ulna.

M. extensor digitorum communis (Figs. 2A, 3B; e d c). This long, narrow muscle arises by a strong tendon from the lateral epicondyle of the humerus superficial to the origin of M. supinator. A small tendinous ulnar anchor in this muscle arises from the tendon of origin, passes caudally, and inserts on the ulna proximal to, and parallel with, the ulnar anchor of M. extensor metacarpi ulnaris. The large belly extends two-thirds the distance down the forearm and ends on a well-developed tendon. The latter passes over the distal end of the ulna dorsally through a fibrous loop and then divides near the proximal end of the carpometacarpus. One branch passes cranially and inserts on the caudal surface of the alular phalanx about 5 mm from the proximal end of the bone. The longer branch continues distally and curves caudally in a groove on the dorsal surface of the carpometacarpus. It then passes deep to a ligamentous loop at the distal end of the carpometacarpus and turns cranioventrally to insert on the cranioventral corner of the proximal end of the first phalanx of the major digit.

M. supinator (Fig. 2A; s). This muscle arises by a well-developed tendon from a shallow depression near the lateral epicondyle of the humerus just deep to the tendon of origin of M. extensor digitorum communis. The fan-shaped belly passes distally to a fleshy insertion on the craniodorsal surface of the proximal half of the radius.

M. extensor indicis longus (*M. extensor longus digiti majoris*) (Figs. 2A, C; 3B; 4A, C; e i l). The slender belly of this muscle arises by both fleshy and tendinous fibers from most of the caudal surface of the radius. The belly ends on a tendon that passes distally between the distal end of the ulna and the os radiale. The tendon continues through a small cartilage that is bounded by the carpometacarpus, the radiale, the ulnare, and the distal end of the ulna and passes into the hand. The tendon proceeds cranially along the dorsal surface of the carpometacarpus and inserts on the cranial surface of the proximal end of the second phalanx of the major digit. Associated with the main tendon is a flat, ligamentous band that passes distally from the wrist cartilage caudal to the main tendon. This band fuses with the main tendon just before it inserts. The main tendon lies in a groove along the cranial edge of this band.

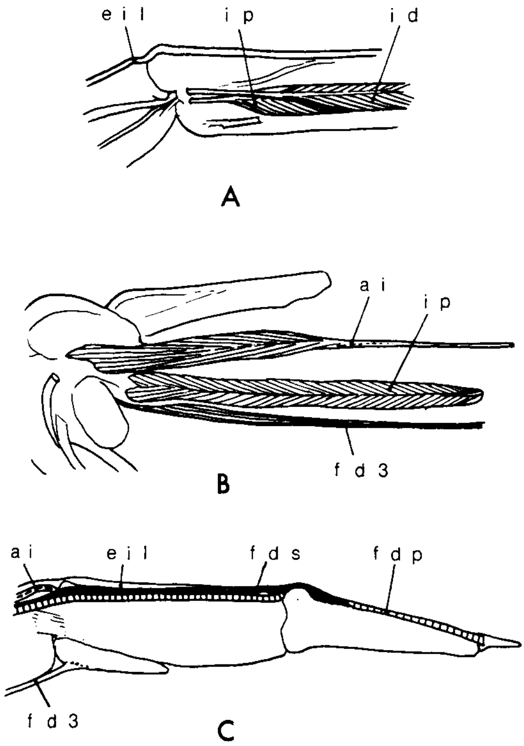

FIGURE 4. Muscles of the left manus of *Camptorhynchus*. (A) Dorsal view. (B and C) Ventral views. (C) Tendon of M. flexor digitorum superficialis black; tendon of M. flexor digitorum profundus crosshatched; tendon of M. abductor indicis dashed.

As noted by George and Berger (1966: 367), a distal head may also be present. In *Camptorhynchus* the distal head lies caudal to the belly of M. extensor pollicis brevis. It arises fleshy from the caudodorsal surface of the proximal end of the major metacarpal and from a ligamentous capsule that attaches to the caudodorsal surface of the os radiale. The small, spindle-shaped belly ends on a thread-like tendon. We could not trace this tendon to the main tendon of insertion.

M. extensor pollicis longus (*M. extensor longus alulae*) (Figs. 1C, 2A, C, 3B; e p l).

As in most birds, this muscle has two heads of origin. The ulnar head has a fleshy origin along the proximal 2-3 mm of the cranial surface of the ulna. The radial head arises fleshy from the caudal surface of the proximal end of the radius and, more distally, from the caudodorsal surface of the radius. These heads join at about the distal end of the proximal one-third of the forearm. The common belly passes distally and ends on a strong, narrow tendon that inserts on the dorsal surface of the distal end of the tendon of insertion of M. extensor metacarpi radialis.

M. ulnimetacarpalis dorsalis (*M. ulnometacarpalis dorsalis*) (Fig. 3B; u d). This well-developed muscle arises by a short tendon from the dorsal surface of the distal end of the ulna. The belly passes distally a few millimeters to a fleshy insertion on the caudodorsal surface of the proximal end of the minor metacarpal, opposite the insertion of M. extensor metacarpi ulnaris. The insertion extends from near the proximal end of the minor metacarpal to the curve of the dorsal edge of that bone.

M. extensor pollicis brevis (*M. extensor brevis alulae*) (Fig. 3B; e p b). This short, fan-shaped muscle arises fleshily from the dorsal surface of the extensor process of the carpometacarpus. The fibers converge onto a strong tendon that inserts on the proximocranial corner of the alular phalanx.

M. abductor pollicis (*M. abductor alulae*) (Fig. 3A; ab p). This small, spindle-shaped muscle arises from the ventral edge of the tendon of insertion of M. extensor metacarpi radialis. The muscle has a fleshy insertion along most of the cranioventral surface of the alular phalanx. The muscle is strongly unipennate with many fibers passing between parallel aponeuroses of origin and insertion.

M. adductor pollicis (*M. adductor alulae*) (Fig. 3B; ad p). This short block of muscle arises by semitendinous fibers from the cranioventral surface of the proximal portion of the major metacarpal. The belly passes cranially and inserts on the caudal surface of the alular phalanx just ventral to the branch tendon of insertion of M. extensor digitorum communis.

M. flexor pollicis (*M. flexor alulae*) (Fig. 3A; f p). This small muscle arises by both fleshy and tendinous fibers from a small depression proximal and cranial to the pisiform process of the carpometacarpus, caudal to the belly of M. abductor pollicis. The fleshy fibers attach to a short tendon that inserts on the ventral corner of the proximal end of the alular phalanx.

M. abductor indicis (*M. abductor digiti majoris*) (Figs. 3A, B, 4B, C; a i). This muscle arises fleshy from the carpometacarpus beginning at the level of the pisiform process where it lies deep to M. flexor pollicis, and, more distally, from the cranial surface of the major metacarpal. The belly ends on a strong tendon that inserts on the cranial surface of the proximal end of the first phalanx of the major digit. The insertion (not shown) lies between the tendons of insertion of M. extensor indicis longus and M. flexor digitorum superficialis.

M. interosseus dorsalis (*M. interosseous dorsalis*) (Fig. 4A; i d). This bipennate muscle has a fleshy origin along the dorsal surface of the proximal portion of the carpometacarpus and the facing surfaces of the major and minor metacarpals. The tendon of insertion proceeds through a fibrous canal at the distal end of the carpometacarpus, passes along the dorsal surface of the first phalanx in a shallow groove, and attaches on the craniodorsal corner of the second phalanx of the major digit. A cartilaginous thickening of the tendon occurs at the interphalangeal joint. From this thickening the slender tendon passes distally along the craniodorsal edge of the second phalanx to insert on the proximodorsal edge of the small third phalanx.

M. interosseus palmaris (*M. interosseous ventralis*) (Figs. 3A, 4A, B; i p). This muscle is as well-developed as M. interosseus dorsalis. The bipennate belly occupies the intermetacarpal space and ends on a tendon that passes to the dorsal side of the wing through a bony canal at the distal end of the carpometacarpus. The insertion is on the caudal edge of the second phalanx of the major digit.

M. flexor digiti III (*M. flexor digiti minoris*) (Figs. 3A, 4B, C; f d 3). This muscle arises fleshy from most of the caudal surface of the carpometacarpus. The proximal portion of the belly is bipennate, but beyond the level of insertion of M. ulnimetacarpalis dorsalis, the fiber arrangement is unipennate. The insertion is by a short tendon as well as by fleshy fibers on the caudal surface of the proximal end of the minor digit.

MUSCLES OF THE HINDLIMB

M. gastrocnemius (Fig. 5D; g). The tendon of this muscle becomes thickened and slightly wider as it passes over the caudal surface of the tibial cartilage (t c). The insertion is on the caudal surface of the hypotarsus along most of its length.

M. tibialis anterior (*M. tibialis cranialis*)

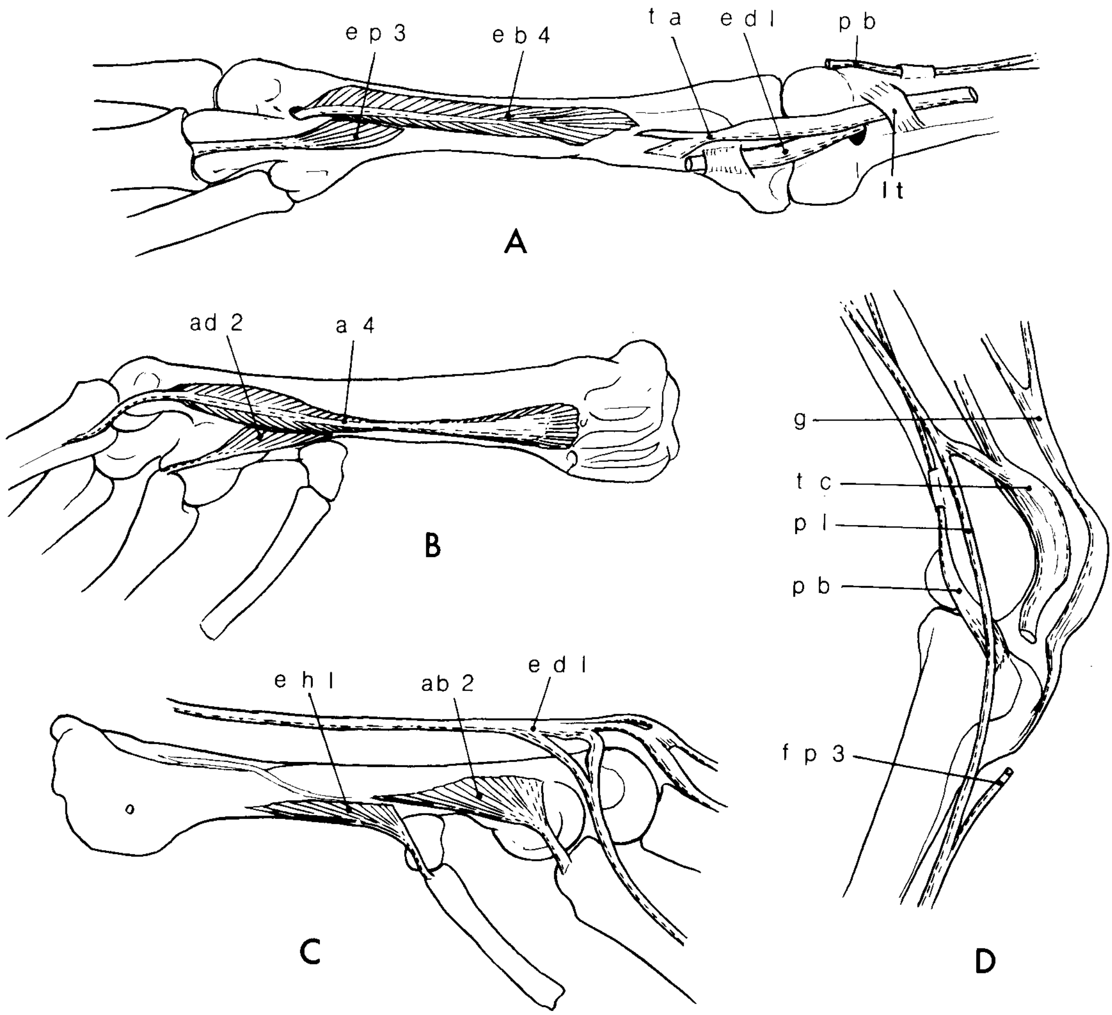

FIGURE 5. Muscles of the tarsometatarsus of *Camptorhynchus*. (A) Cranial view, right leg. (B) Caudolateral view, left leg. (C) Medial view, left leg; tendon of M. extensor digitorum longus displaced. (D) Lateral view of ankle joint, left leg; tendon of M. gastrocnemius displaced.

(Fig. 5A; t a). The tendon of this muscle passes deep to the ligamentum transversum (l t) lateral to the tendon of M. extensor digitorum longus. It widens slightly as it continues distally and crosses the intertarsal joint. The tendon tapers slightly, then broadens and divides just before it inserts on the cranial surface of the proximal end of the tarsometatarsus.

M. extensor digitorum longus (Figs. 5A, C; e d l). The tendon of this muscle passes through a bony canal that is deep to the ligamentum transversum. It then proceeds distally medial to the tendon of M. tibialis anterior and passes through a second fibrous loop on the cranial surface of the proximal end of the tarsometatarsus. At the distal end of the tarsometatarsus the tendon divides, sending a branch to the dorsal surface of each of the three foretoes. Owing to the brittle condition of the specimen the pattern of insertion of this tendon could not be determined with confidence.

M. peroneus longus (*M. fibularis longus*) (Fig. 5D; p l). The tendon of this muscle passes along the lateral surface of the tibiotarsus and divides near the distal end of that bone. One branch passes caudally and fuses with a dense fascial sheet on the lateral surface of the tibial cartilage. The main tendon crosses the intertarsal joint and fuses with the tendon of M. flexor perforatus digiti III near the distal end of the proximal one-third of the tarsometatarsus.

M. peroneus brevis (*M. fibularis brevis*) (Figs. 5A, D; p b). The tendon of this muscle passes through a fibrous canal on the lateral surface of the distal end of the tibiotarsus

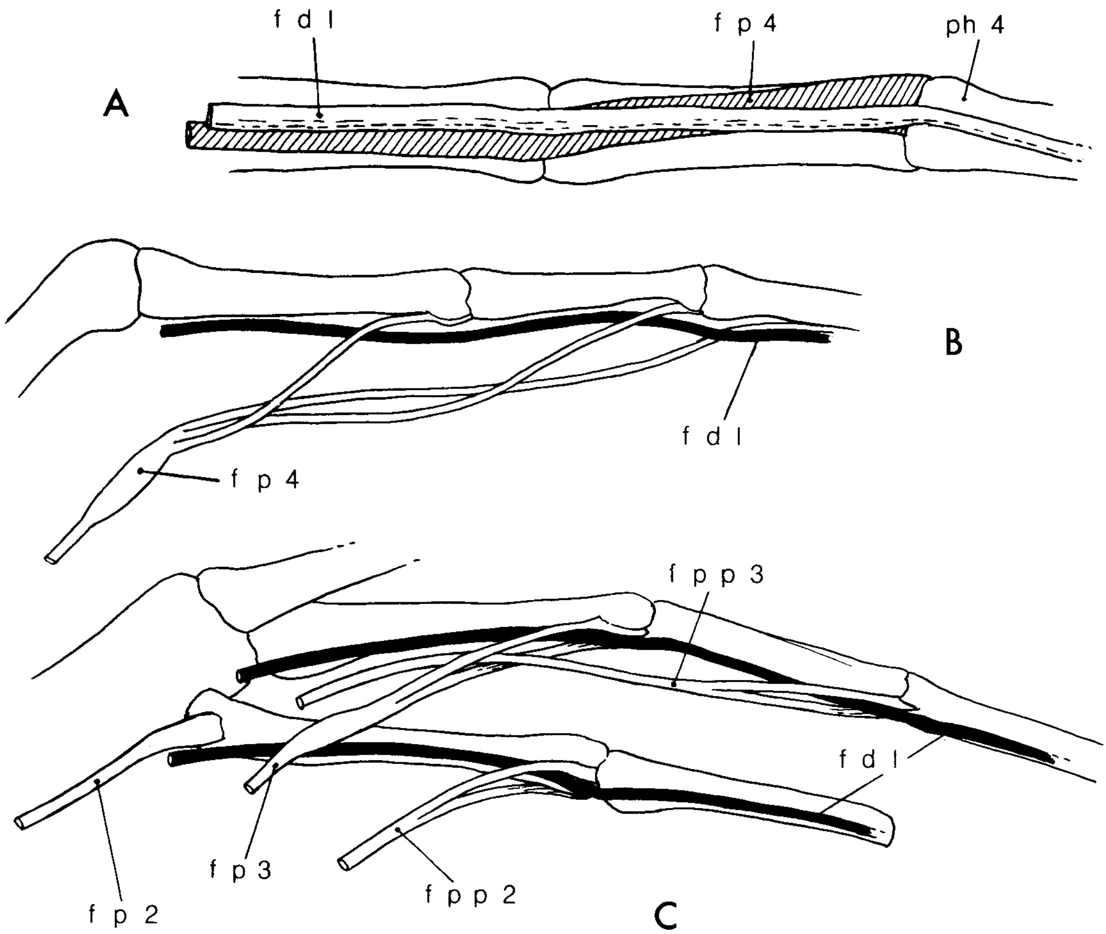

FIGURE 6. Plantar tendons of right foot of *Camptorhynchus*. (A) Ventral view of digit IV, tendon of M. flexor perforatus digiti IV crosshatched. (B) Lateral view of digit IV. (C) Lateral view of digits II and III, tendons displaced for clarity; branch tendons of M. flexor digitorum longus black.

and crosses the intertarsal joint. The insertion is on the caudolateral surface of the proximal end of the tarsometatarsus.

M. flexor perforans et perforatus digiti III (Figs. 6C, 7; f p p 3). The tendon of this muscle passes through a large, caudolateral canal of the tibial cartilage and along the hypotarsus in company with the tendons of M. flexor perforatus digiti III and M. flexor perforatus digiti IV. It then receives a small tendinous branch from the tendon of M. flexor perforatus digiti III and continues distally along the caudal surface of the tarsometatarsus. The tendon passes along a cartilaginous pad at the base of digit III, perforates the tendon of M. flexor perforatus digiti III, and then divides at the distal end of the first phalanx, allowing for the passage of the branch tendon of M. flexor digitorum longus. The insertion is on the lateral and medial surfaces of the proximal end of the third phalanx of digit III.

M. flexor perforans et perforatus digiti II (Figs. 6C, 7; f p p 2). The tendon of this muscle passes through a caudomedial canal of the tibial cartilage and along a tendinous groove on the caudomedial surface of the hypotarsus. It proceeds distally along the tarsometatarsus and divides at about the midpoint of the first phalanx, allowing for the passage of the branch tendon of M. flexor digitorum longus. The tendon passes distally ventral to the branch tendon of M. flexor digitorum longus and inserts on the lateral and medial surfaces of the proximal end of the second phalanx of digit II.

M. flexor perforatus digiti IV (Figs. 6A, B, 7; f p 4). The tendon of this muscle passes through a large caudolateral canal of the tibial cartilage in company with the tendons of M. flexor perforatus digiti III and M. flexor perforans et perforatus digiti III. It then passes along a groove on the caudolateral surface of the hypotarsus. It continues distally along the caudal surface of the tarsometatarsus and becomes thickened as it passes ventral to a cartilaginous pad at the base of the fourth toe. The tendon divides at the proximal end of the first phalanx. The two most proximal branches insert, respectively, on the lateral surface of the distal end of the first phalanx and on the lateral surface of the distal end of the second phalanx. The medial and most distal branch passes dorsal to the branch of M. flexor digitorum longus and inserts on the plantar surface of the proximal end of the fourth phalanx.

M. flexor perforatus digiti III (Figs. 5D, 6C, 7; f p 3). The tendon of this muscle passes through the tibial cartilage and along the hypotarsus in company with the tendons of M. flexor perforatus digiti IV and M. flexor perforans et perforatus digiti III. It then receives the main tendon of M. peroneus longus, and shortly sends a small branch to the tendon of M. flexor perforans et perforatus digiti III. The main tendon then thickens and divides allowing for the passage of the tendon of M. flexor perforans et perforatus digiti III and the branch tendon of M. flexor digitorum longus. The main insertion is on the medial and lateral surfaces of the proximal end of the second phalanx of digit III. Both branches are also tightly bound to the distal end of the first phalanx.

It was difficult to determine whether or not the tendinous connection between the tendons of M. flexor perforans et perforatus digiti III and M. flexor perforatus digiti III was the vinculum as described by Hudson (1937). Such a structure has been found in ducks (George and Berger 1966:433; Raikow 1970: Fig. 17).

M. flexor perforatus digiti II (Figs. 6C, 7; f p 2). The tendon of this muscle passes through a central canal of the tibial cartilage and through a central groove of the hypotarsus. It proceeds down the tarsometatarsus lateral to the tendon of M. flexor perforans et perforatus digiti II. After becoming thickened, it inserts on the proximolateral corner of phalanx one of digit II where it is bound to a cartilaginous pad associated with that digit. The tendon is neither perforated nor does it perforate any other tendon.

When we dissected the tendons of M. flexor perforatus digiti IV, M. flexor perforatus digiti III, and M. flexor perforans et perforatus digiti III, we noticed a loop in each tendon near the base of the toes. The presence of these loops in the flexor tendons of both feet was initially puzzling as we found none in a specimen each

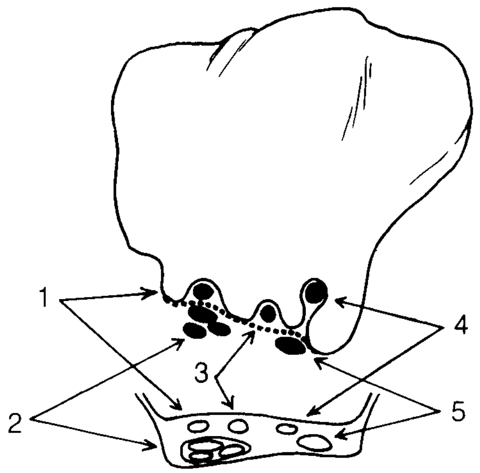

FIGURE 7. Left hypotarsus and tibial cartilage of *Camptorhynchus*; semidiagrammatic. In life, tibial cartilage would be proximal to (superimposed on) hypotarsus. Dotted line represents a sheet of connective tissue. Black ovals represent tendons in relation to hypotarsus; open ovals show their relations to tibial cartilage. (1) M. flexor hallucis longus; (2) M. flexor perforatus digiti III (above), M. flexor perforatus digiti IV (lower left), M. flexor perforans et perforatus digiti III (lower right); (3) M. flexor perforatus digiti II; (4) M. flexor digitorum longus; (5) M. flexor perforans et perforatus digiti II.

of the Oldsquaw, the scoter, and the eider and they are unknown in other birds. Most tendons of the left foot except that of M. flexor digitorum longus were destroyed in cleaning the bones before we first saw the loops. A small loop on one branch of the tendon of M. flexor digitorum longus of that foot, however, suggested that loops on other tendons may have been present, as in the right foot. An examination of the feet (stuffed and resewn by Humphrey and Butsch) of the study skin revealed small holes in the podothecae of both feet in precisely the positions to be expected if a needle or wire had been passed through the feet (and tendons) during the initial preparation of the specimen. We believe that the loops in the tendons are artifacts of preparation.

M. flexor digitorum longus (Figs. 6A, B, C, 7; f d 1). The tendon of this deep flexor muscle passes through a canal of the tibial cartilage and then through the medial canal of the hypotarsus. It then passes distally along the caudal surface of the tarsometatarsus, receives the tendon of M. flexor hallucis longus, and divides at a point about half the distance between the level of the hallux and the distal end of the tarsometatarsus, sending branches to all of the foretoes. At the distal end of the tarsometatarsus, each branch tendon passes ventral to a cartilaginous pad and is held in place by a sheath of connective tissue that attaches along the lateral and medial edges of each pad, as well as the proximoventral ridges of each basal phalanx. The branch to digit II perforates the tendon of M. flexor perforans et perforatus digiti II and continues distally along the plantar surface of the second phalanx past its distal end. The branch to digit III perforates the tendon of M. flexor perforatus digiti III and continues distally to perforate the tendon of M. flexor perforans et perforatus digiti III. The tendon proceeds along the plantar surface of digit III beyond the distal end of the third phalanx. The branch to digit IV lies in a groove on the lateral surface of the tendon of M. flexor perforatus digiti IV at the proximal end of the basal phalanx. The tendon passes between the distal two branches of the tendon of M. flexor perforatus digiti IV and proceeds distally, ventral to the most medial branch of that tendon. The tendon continues along the plantar surface of digit IV past the distal end of the fourth phalanx. The ungual phalanges and insertions of the branch tendons were missing. Accessory vincula could not be found.

M. flexor hallucis longus (Fig. 7). In *Camptorhynchus* the tendon of this muscle was present only in its role of assisting the tendon of M. flexor digitorum longus. A branch to the hallux could not be found. In *Somateria mollissima* we found that the tendon passed through a lateral canal of the tibial cartilage and through the lateralmost groove of the hypotarsus.

M. extensor hallucis longus (Fig. 5C; e h 1). This small muscle arises fleshy from the medial surface of the tarsometatarsus just proximal to the midpoint of that bone. The fibers of the belly converge on a short tendon that inserts on the dorsal surface of the proximal end of the hallux.

M. adductor digiti II (Fig. 5B; ad 2). This small, bipennate muscle has a fleshy origin on the caudal surface of the tarsometatarsus distal to the level of the hallux and medial to the belly of M. abductor digiti IV. The belly ends on a tendon that passes under two strong ligaments and inserts on the proximomedial surface of the first phalanx of digit II. Statements about the true extent of muscle origin are tenuous in small muscles such as this, owing to shrinkage from drying.

M. abductor digiti IV (Fig. 5B; a 4). This muscle arises from a depression in the caudal surface of the tarsometatarsus that extends from the hypotarsus to the trochleae. Proximally the belly is fan-shaped, its fibers converging on a broad, superficial aponeurosis. Distally, the bipennate belly widens again before giving rise to a tendon that inserts on the ventrolateral surface of the proximal end of the first phalanx of digit IV.

M. abductor digiti II (Fig. 5C; ab 2). This small, fan-shaped muscle arises fleshy from the distomedial surface of the tarsometatarsus between the hallux and the medial trochlea. The belly ends on a stout tendon that inserts on the medial surface of the proximal end of the first phalanx of digit II.

M. extensor proprius digiti III (Fig. 5A; e p 3). Small and fan-shaped, this muscle has a fleshy origin from the cranial surface of the distal one-third of the tarsometatarsus. The short tendon passes over the trochlea and inserts on the dorsal surface of the proximal end of the first phalanx of digit III.

M. extensor brevis digiti IV (Fig. 5A; e b 4). This bipennate muscle arises by both fleshy and tendinous fibers from the cranial surface of the tarsometatarsus at the level of the insertion of M. tibialis anterior. The belly ends on a tendon that passes through the distal foramen of the tarsometatarsus and inserts on the dorsal surface of the proximomedial corner of the first phalanx of digit IV.

We were unable to find M. flexor hallucis brevis, M. lumbricalis, and the tendon of insertion of M. plantaris in our specimen of *Camptorhynchus*. This was probably due to the dried and brittle condition of the muscles.

DISCUSSION

The presence of M. entepicondyloulnaris in ducks was first reported by Sy (1936), who described and illustrated it in *Casarca* (= the Ruddy Sheld-Duck, *Tadorna ferruginea*?). Its presence also in *Camptorhynchus labradorius*, *Melanitta deglandi*, *Clangula hyemalis*, and *Somateria mollissima*, demonstrated here, suggests that this muscle occurs widely in the Anatidae. The muscle is presently known only in *Apteryx*, Tinamidae, Galliformes, and Anatidae. Although it appears to be a primitive feature in birds, its taxonomic significance cannot be determined without documenting its presence or absence in other avian families.

Our study sheds no light on the affinities of the Labrador Duck owing to the lack of any comparative study of the myology of the sea ducks. Several features of the carpometacarpus and tarsometatarsus, however, provide taxonomic clues. Woolfenden (1961:32–33) pointed out that a basic difference in the shape of the process of metacarpal I divides the sea ducks into two groups: (1) *Bucephala* and the mergansers, and (2) the eiders, scoters, *Histrionicus* and *Clangula*. In this character *Camptorhynchus* clearly falls within the second group. We have found that the position of the nutrient foramen of the tarsometatarsus, as seen just distal to the hypotarsus, also separates the two groups of sea ducks. In the first group the foramen lies lateral to the long axis of the lateral groove of the hypotarsus (housing the tendon of M. flexor hallucis longus); in the second, the foramen lies on or medial to the axis of that groove. Again, *Camptorhynchus* resembles the eiders, scoters, and their relatives in this respect.

Woolfenden (1961:85) listed several characters of the tarsometatarsus by which eiders could be distinguished from other ducks; we found that *Camptorhynchus* agrees well with those given for eiders. However, we did not find the curvature of the external edge of the shaft to be notably different between eiders and scoters. Spreading of the trochleae was not easily discernible except through the shape of the space between the trochleae for digits III and IV. In scoters, the opposite sides of these trochleae tend to be straight and parallel, enclosing a relatively narrow space; in eiders and *Camptorhynchus*, the opposite sides are each somewhat concave, enclosing a more oval and wider space. In *Camptorhynchus* the minimum width of the shaft was 9.0% of the total length, near the middle of the range (8.5–9.8%) given by Woolfenden for eiders.

Woolfenden (1961:33) also listed characters of the carpometacarpus that he believed separated the eiders from scoters and the Harlequin Duck (*Histrionicus histrionicus*). Of these we found the more distal attachment of M. extensor metacarpi ulnaris (his "flexor") and the slight curvature of metacarpal II from medial (our ventral) view to be generally characteristic of the eiders, although each feature is variable in both eiders and scoters. *Camptorhynchus* matches the eiders in both features. *Histrionicus* and *Clangula* differ from *Camptorhynchus* in having a straight metacarpal II. In *Camptorhynchus* we also found that the dorsal edge of metacarpal III curves ventrally (from caudal view) as it approaches its proximal junction with metacarpal II. In *Histrionicus, Clangula*, and most specimens of scoters, the proximodorsal edge runs almost parallel to the dorsal edge of metacarpal II.

Delacour and Mayr (1945:33) remarked that *Camptorhynchus* "seems to be about halfway between the eiders and the Oldsquaw." In the Check-list of North American Birds (A. O. U. 1957), the Labrador Duck is placed between the Harlequin Duck and the eiders, and Palmer (1976) put it between the scoters and the Harlequin Duck. Humphrey and Butsch (1958) put *Camptorhynchus* in the Mergini between *Melanitta* and *Clangula*, and they removed the eiders from that tribe. Based on an illustration of the sternum in Rowley (1877), Woolfenden (1961:45) stated that "the sternum resembles that of the eiders in that the posterior lateral processes are wide, and in line with the long axis of the element, and it lacks the basal curvature possessed by the scoters. However, the sternum appears less specialized than in the eiders, for the posterior lateral processes approach the xiphisternum, as in *Histrionicus*." We found the sternum of the Labrador Duck to most closely resemble that of the Steller's Eider (*Polysticta stelleri*). From a description of the trachea by Wilson (1829), Johnsgard (1965: 270) concluded that the "asymmetrical and osseus bulla is unlike that of the scoters, and the only other sea ducks with such bullae are the eiders and the Harlequin Duck. This suggests that the Labrador Duck might provide an evolutionary link between the eiders and such other sea ducks as the harlequin and the scoters." The presence of skeletal characters unique to eiders and the Labrador Duck leads us to regard the eiders as the nearest living relatives of the Labrador Duck.

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GLOSSARY OF ABBREVIATIONS

FORELIMB

a	M. anconeus
ab p	M. abductor pollicis
ad p	M. adductor pollicis
a i	M. abductor indicis
b	M. brachialis
e	M. entepicondyloulnaris
e d c	M. extensor digitorum communis
e i l	M. extensor indicis longus
e m r	M. extensor metacarpi radialis
e m u	M. extensor metacarpi ulnaris
e p b	M. extensor pollicis brevis
e p l	M. extensor pollicis longus
f c u	M. flexor carpi ulnaris
f d 3	M. flexor digiti III
f d p	M. flexor digitorum profundus
f d s	M. flexor digitorum superficialis
f p	M. flexor pollicis
h c	humerocarpal band
ht	M. humerotriceps
i d	M. interosseus dorsalis
i p	M. interosseus palmaris
l c v	ligamentum collaterale ventrale
p p	M. pronator profundus
p s	M. pronator superficialis
s	M. supinator
st	M. scapulotriceps
u a	ulnar anchor
u d	M. ulnimetacarpalis dorsalis
u v	M. ulnimetacarpalis ventralis

HINDLIMB

a 4	M. abductor digiti IV
ab 2	M. abductor digiti II
ad 2	M. adductor digiti II
e b 4	M. extensor brevis digiti IV
e d l	M. extensor digitorum longus
e h l	M. extensor hallucis longus
e p 3	M. extensor proprius digiti III
f d l	M. flexor digitorum longus
f p 2	M. flexor perforatus digiti II
f p 3	M. flexor perforatus digiti III
f p 4	M. flexor perforatus digiti IV
f p p 2	M. flexor perforans et perforatus digiti II
f p p 3	M. flexor perforans et perforatus digiti III
g	M. gastrocnemius
l t	ligamentum transversum
p b	M. peroneus brevis
ph 4	phalanx 4
p l	M. peroneus longus
t a	M. tibialis anterior
t c	tibial cartilage

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