

Toe Extensors and Flexors of Tibetan Snowcock

(Aves, Phasianidae)

By

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The snowcocks, with five species belonging to the genus *Tetraogallus*, inhabit alpine pastures and barren slopes of mountains of central Asia from Asia Minor to western China. They are true members of the pheasant family, but approach the ptarmigans in habitat and behavior (cf. ALI and RIPLEY, 1969, pp. 10–16; BAKER, 1928, pp. 426–432; DEMENT'EV *et al.*, 1967, pp. 198–221).

The Phasianidae (pheasants, quails, and partridges) and the Tetraonidae (grouse and ptarmigans) are closely related families. Anatomical and external morphological features that distinguish the two taxa are few, and some authors consider the Tetraonidae to warrant only subfamilial recognition within the Phasianidae (SHORT, 1967). One myological feature, *i.e.*, the absence of the adductor digiti II muscle in the foot, appears to be peculiar to the Tetraonidae among the galliform birds (HUDSON *et al.*, 1959, 1966) and is considered to be of great taxonomic importance. Although it seems to be a trivial difference, its taxonomic value depends largely upon the variation of this muscle in the galliforms. The prime purpose of this study is to examine the muscle in *Tetraogallus* and some other genera of the Phasianidae (*Alectornis*, *Perdix*) that appear to be intermediate between the two families. The toe extensors and flexors of *Tetraogallus* are described and a few comparative remarks are given.

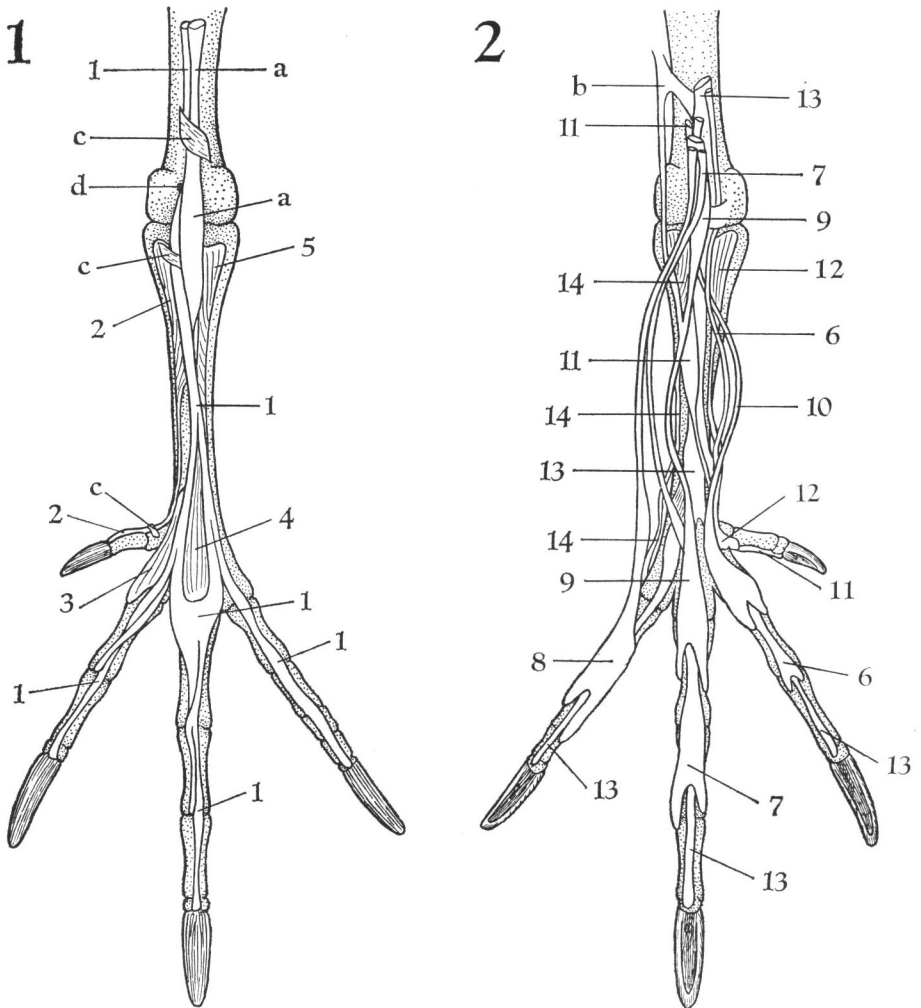
Material. The material used in this study consisted of three frozen birds of the Tibetan Snowcock (*Tetraogallus tibetanus*) imported from China. The birds were purchased for skeletal specimens, but their flesh was found to be quite satisfactory for anatomical examination. The six legs of the specimens were first injected with 5% formalin and preserved in 75% ethyl alcohol. Specimens of the Hazel Grouse (*Tetrastes bonasia*, 2 legs), Chukar Partridge (*Alectornis chukar*, 2 legs), Daurian Partridge (*Perdix dauuricae*, 2 legs), Quail (*Coturnix japonica*, 2 legs), and Domestic Fowl (12 legs) were dissected for comparison.

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Description for *Tetraogallus*

The muscles inserting on the phalanges of the toes fall into the extensor group of

five muscles and the flexor group of ten muscles. Their topographical relationships on the foot are shown in Figs. 1 and 2. These muscles act to extend or flex the toes and exercise fine control of the phalanges. Those toe extensors and flexors arising from the tibiotarsus contribute also to the flexion or extension of the tarsometatarsus.



Figs. 1-2. *Tetraogallus tibetanus*. — 1. Anterior view of left foot showing superficial muscles. — 2. Posterior view of left foot showing superficial muscles. See Fig. 3 for explanation.

The pelvic limb muscles of *Tetraogallus* are, in general, extremely similar to those of the grouse as described in detail by HUDSON *et al.* (1959) for *Dendragapus* (Blue Grouse). I dissected specimens of *Tetrastes* (Hazel Grouse) and concur with most of

HUDSON's description.

1) *M. extensor digitorum longus* (*M. ext. dig. l.*)

This muscle lies deep to *M. tibialis anterior*, extending from the proximal end of the tibiotarsus along the anterior surface of the bone. Its origin is almost entirely fleshy from the groove formed by the outer and inner cnemial crests and from the proximal fourth of the anterolateral surface of the tibiotarsus. Fibers also arise from the fascia covering the medial surface of the muscle. Its belly narrows distally into a stout tendon of insertion, which lies posteromedial to the tendon of *M. tibialis anterior* at the distal end of the tibiotarsus. In the region of the intertarsal joint the tendon passes through two fibrous loops and a bony canal so that it is held tightly against the surface of the shafts of the tibiotarsus and tarsometatarsus. About half way down the tarsometatarsus the tendon flattens and bifurcates into two main branches. Each of the main branches of tendon again bifurcates at a level about four-fifths the way down the tarsometatarsus, and the most lateral branch inserts on the anterior surfaces of the phalanges of digit IV. The most medial branch divides into two distinct flat tendons that terminate on the bases of phalanx 2 and of the claw respectively. The middle two branches, one from the inner and the other from the outer main branches, fuse together at the tarsometatarsal joint and supply digit III. Although these branches of tendon are not difficult to trace, they are incorporated into the sheet of fibrous tissue continuously covering the tarsometatarsal joints and the surfaces of the front toe digits. The main branches are also connected by a tendinous sheet.

The contraction of *M. ext. dig. l.* extends all digits except the hallux simultaneously. It also flexes the tarsometatarsus. The muscle has a complex structure. The tendon of insertion is situated along the posterior (deep) surface of the muscle, extending into the distal two-thirds of the belly. Fiber arrangement on this tendon is bipinnate with fibers inserting from the medial fascia and an aponeurosis on the anterolateral side of the muscle. Proximally, the fibers have also a bipinnate arrangement; the medial fibers from the inner cnemial crest and the medial fascia and the lateral fibers from the outer cnemial crest insert bipinnately onto the anterolateral aponeurosis.

2) *M. extensor hallucis longus* (*M. ext. hal. l.*)

This muscle extends from the proximal end of the tarsometatarsus to the hallux (digit I) along the anteromedial side of the bone. Its origin is fleshy from the anteromedial surface of the proximal head of the tarsometatarsus medial to the fibrous loop holding the tendon of *M. ext. dig. l.* It also arises by flesh fibers from the medial part of the anterior tarsal groove and from a narrow line on the anterior surface of the tarsometatarsus distal to the insertion of *M. tibialis anterior*. The latter origin extends about half to two-thirds the way down the bone. The muscle inserts upon the upper surface of the hallux by a thin but stout tendon which ends on the base of the claw.

The shortening of *M. ext. hal. l.* extends the hallux. This is a flat muscle with

the tendon of insertion lying along its medial edge. Fiber arrangement on this tendon is unipinnate except for the very proximal part of origin. The short distal head of *M. ext. hal. I.* (cf. HUDSON *et al.*, 1959, p. 38) appears to be absent.

3) *M. abductor digiti II (M. abd. dig. II)*

This is a short muscle lying on the medial side of the distal part of the tarsometatarsus, and is medial to *M. ext. pro. d. III.* The origin is fleshy from the medial surface of the bone distal to the tendon of *M. ext. hal. I.* extending obliquely to the base of the hallux. Few fibers arise from the base of metatarsal I. It has an insertion by a flat tendon on the medial side of the base of phalanx I (of digit II). The tendon of insertion extends over the medial (superficial) surface of the muscle as an aponeurosis, and fibers insert unipinnately onto it.

This muscle rotates the second toe inward (mediad). CRACRAFT (1971, p. 239) stated that the muscle has a variety of roles, *i.e.*, it acts as a flexor of phalanx I (of digit II) when the phalanx is already in a flexed position and as an extensor if the phalanx is in the extended position. As he mentioned, the tendon is not fixed in place but can slide over the surface of the trochlea. In *Tetraogallus*, however, the slide movement of the tendon is such that the muscle probably acts as a weak extensor if the phalanx is in the flexed position and only as the abductor of the second toe if the phalanx is extended. It is doubtful that the muscle has any power of flexion.

4) *M. extensor proprius digiti III (M. ext. pro. d. III)*

This short muscle lies on the distal part of the anterior surface of the tarsometatarsus. It is situated beneath the sheet of fibrous tissue connecting the two main branches of *M. ext. dig. I.* and has a very flat belly. The origin is entirely fleshy from the distal fourth of the anterior surface of the tarsometatarsus. The tendon of insertion is incorporated into the capsule tissue of the tarsometatarsal joint and inserts upon the anterior surface of the base of phalanx I (of digit III). Fibers insert directly on the capsule tissue and the muscle has a structure close to a parallel-fibered muscle. This is a weak extensor of digit III. In some specimens of *Tetraogallus* this muscle is obsolete.

5) *M. extensor brevis digiti IV (M. ext. brev. d. IV)*

This slender and flat muscle extends from the proximal end of the tarsometatarsus to phalanx I of digit IV along the median line on the anterior surface of the tarsometatarsus. Its origin is fleshy from the medial side of the lateral ridge of the anterior tarsal groove and extends about half way down the shaft of the bone. The tendon of insertion passes through a bony canal between trochleae 3 and 4, and inserts on the medial side of the base of phalanx I (of digit IV). This is a unipinnate muscle (except the proximal part of origin) with the flat tendon of insertion extending along nearly the entire anterior (superficial) surface of the muscle. The muscle structure is similar to that of *M. ext. hal. I.*, but the fibers are shorter and fewer.

The shortening of *M. ext. brev. d. IV* rotates digit IV inward (mediad) or resists the outward movement of the digit. The muscle seems to have no power of extending the fourth toe (cf. CRACRAFT, 1971, p. 239). When pulling the tendon of insertion by hand with the digit in various extended and flexed positions (all surrounding tissue removed), I observed practically no extension or flexion of the digit.

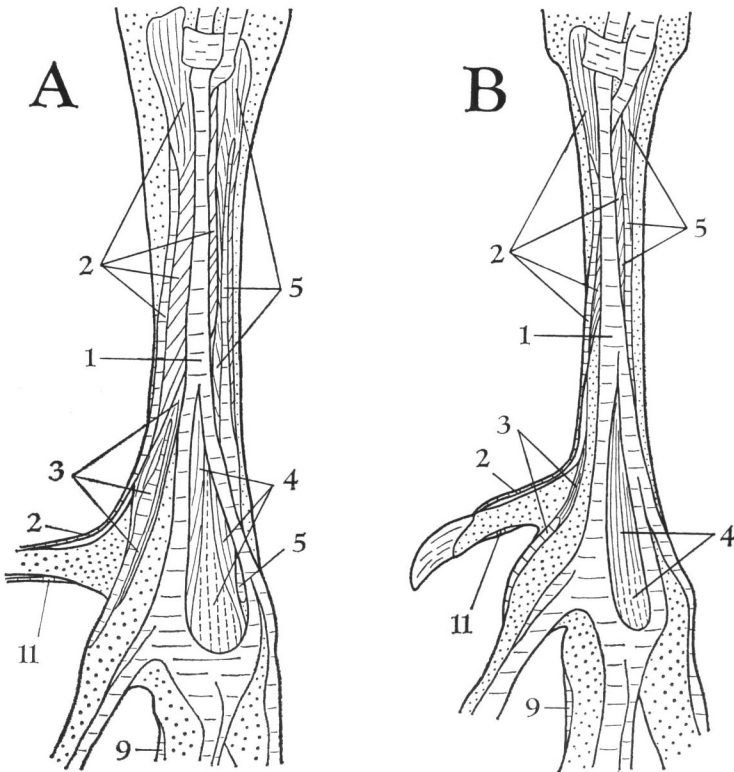
6) *M. flexor perforans et perforatus digiti II (M. flex. pp. d. II)*

This muscle is partly superficial on the posterolateral side of the shank. It takes an aponeurotic origin from the lateral side of the external condyle of the femur and a fleshy origin from the posterolateral surface of the patellar cap. The aponeurosis of origin is shared with *M. flex. pp. d. III*, and the bellies of the two muscles unite in their proximal half. The muscle has a smaller, but distinct, distal head that is separated from the larger lateral head by the belly of *M. flex. pp. d. III*. This part arises from an aponeurosis attached to the edge of the outer cnemial crest. The belly terminates on a slender tendon of insertion about two-thirds the way down the tibiotarsus. The tendon extends obliquely from the lateral to the medial side and passes through its own cartilaginous and bony canals of the tibia in the most posteromedial corner of the intertarsal joint region. At the base of digit II the tendon of this muscle perforates that of *M. flex. per. d. II*, and it is perforated by the tendon of *M. flex. dig. I*, shortly proximal to its insertion upon the posterodistal end of phalanx 2 (of digit II).

This is a flat, basically unipinnate muscle. The tendon of insertion covers almost the entire posterolateral (superficial) surface of the muscle as an aponeurosis, whereas the aponeurosis of origin lies along its anteromedial (deep) surface and is shared with *M. flex. pp. d. III*. Most fibers run from their origin to the insertion unipinnately. The fibers of the distal head arise from the distal part of the aponeurosis from the outer cnemial crest that covers the anteromedial surface of *M. flex. pp. d. III*, and insert on the tendon of insertion unipinnately. This muscle extends the tarsometatarsus and flexes the second toe. CRACRAFT (1971, p. 236) said that, in the domestic pigeon, the muscle has an important role of maintaining posture since it contains a large proportion of tonus fibers.

7) *M. flexor perforans et perforatus digiti III (M. flex. pp. d. III)*

This muscle is situated anteromedial to *M. flex. pp. d. II* and is partially covered by it posterolaterally. It arises partly by flesh fibers from the patellar cap, but mostly from two aponeuroses lying along the posterolateral and the anteromedial sides of the muscle belly respectively. The posterolateral aponeurosis arises from the lateral side of the external condyle of the femur and is shared with *M. flex. pp. d. II* (main portion). The anteromedial aponeurosis attaches to the edge of the outer cnemial crest of the tibiotarsus and is shared with *M. tibialis anterior* (anterior head), *M. flex. dig. I*, and *M. flex. pp. d. II* (distal head). The belly is fused with that of *M. flex. pp. d. II* proximally, and narrows abruptly on a flat tendon of insertion at the middle of the tibiotarsus. The tendon passes the posterior side of the tibial cartilage by



ensheathed in the tendon of *M. flex. per. d. III*, and extends down to the base of the third toe. It lies anterolateral to the tendon of *M. flex. per. d. III* on the posterior surface of the distal part of the tarsometatarsus. The tendon of *M. flex. pp. d. III* perforates *M. flex. per. d. III* and is perforated by *M. flex. dig. I*. much the same way as in *M. flex. pp. d. II*. The tendon ends on the posterodistal end of phalanx 3 (of digit III).

The structure of the muscle is typically bipinnate. The tendon of insertion lies on the medial side of the belly for a short distance and all the fibers from the two aponeuroses of origin insert onto it. The muscle extends the tarsometatarsus and flexes the third toe. There is a short vinculum extending from *M. flex. pp. d. III* to *M. flex. per. d. III* at the level of digit I.

8) *M. flexor perforatus digiti IV (M. flex. per. d. IV)*

This muscle lies deep to *M. gastrocnemius pars externa* and lateral to *M. flex. per. d. III*. It has two heads and a distal slip of origin. The larger medial head arises mainly by an aponeurosis and partly by flesh fibers from the popliteal fossa of the femur. The aponeurosis of origin is common for the medial heads of *per. d. IV, III* and *II*,

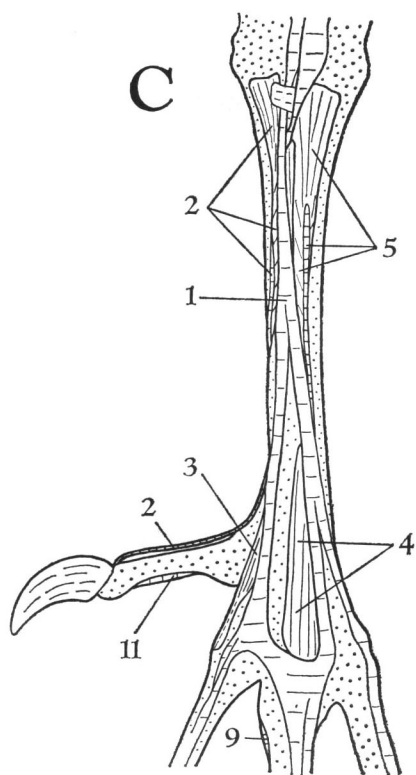
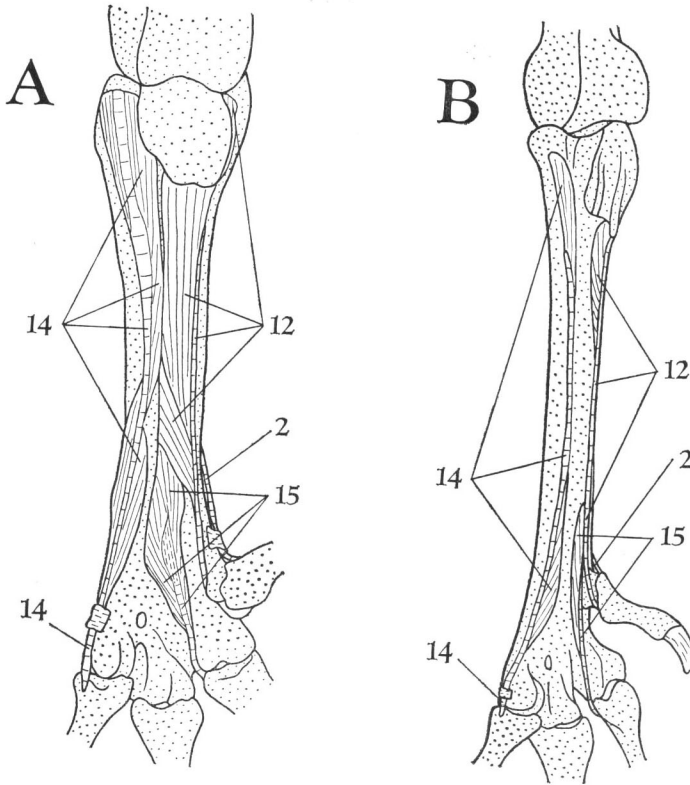


Fig. 3 (on pp. 128–129). Comparison of deepest muscles, anterior view of left foot. — A, *Gallus gallus* (domestic); B, *Tetraogallus tibetanus*; C, *Tetrastes bonasia*.

1, Extensor digitorum longus; 2, Extensor hallucis longus; 3, Abductor digiti II; 4, Extensor proprius digiti III; 5, Extensor brevis digiti IV; 6, Flexor perforans et perforatus digiti II; 7, Flexor perforans et perforatus digiti III; 8, Flexor perforatus digiti IV; 9, Flexor perforatus digiti III; 10, Flexor perforatus digiti II; 11, Flexor hallucis longus; 12, Flexor hallucis brevis; 13, Flexor digitorum longus; 14, Abductor digiti IV; 15, Adductor digiti II; a, Tibialis anterior; b, Peroneus longus; c, fibrous loop; d, bony canal. Figs. 1 and 2 were drawn by direct observation and Figs. 3 and 4 by using a drawing apparatus under a stereoscopic microscope. Slight difference in angle of view must be allowed for Figs. A, B and C in Figs. 3 and 4.

and covers the medial side of per. d. IV and the lateral side of per. d. III. The smaller lateral head takes its origin partly by flesh fibers from the patellar cap, but mainly by an aponeurosis attached to the lateral side of the external condyle of the femur. This aponeurosis is common with the lateral head of per. d. II. The distal slip branching from the middle of the belly arises from the posterior surface of a stout tendon which originates from the patellar cap and is fused with the ambiens tendon distally. This origin is shared with per. d. III (lateral head) and per. d. II (distal slip). The belly extends distally about three-fourths the way down the tibiotarsus. The tendon of insertion is ensheathed by that of per. d. III and lies on the posterior end of the tibial cartilage. It extends down along the posterolateral side of the tarsometatarsus to insert upon the posterior side of the base of phalanx 4 (of digit IV). The tendon has branches inserting on phalanges 1, 2 and 3. Just distal to trochlea 4, the tendon of per. d. III is perforated by that of M. flex. dig. I.

The muscle is closely associated with M. flex. per. d. III and II and has a complex structure. The tendon of insertion lies along the posteromedial edge of the muscle. Fiber arrangement is bipinnate in the medial head and unipinnate in the lateral head. The fibers from the both heads insert directly on the tendon of insertion. The distal



slip has a unipinnate fiber arrangement with the fibers running from the aponeurosis of origin to the aponeurosis that covers the distal half of the posteromedial surface of the belly and confluent with the tendon of insertion.

9) *M. flexor perforatus digiti III* (*M. flex. per. d. III*)

This muscle lies medial to *M. flex. per. d. IV* and is covered by the latter distally. It has two heads of origin. The medial or main head is fused with the medial head of *per. d. IV*, and arises from the medial surface of the common aponeurosis of origin for the medial heads of *per. d. IV*, III and II. The distal, lateral head is partly fused with the distal part of the belly of *per. d. IV*, and takes its origin from the tendon common to the insertion of *M. ambiens* (and also serving as origin for the distal slips of *per. d. IV* and II). The belly of *per. d. III* narrows on a flat tendon of insertion, which becomes broader and ensheathes the tendons of *per. d. IV* and *pp. d. III* as it passes the posterior end of the tibial cartilage. A short distance distal to the hypotarsus the tendon of *per. d. III* receives the tendon of insertion of *M. peroneus longus*. There is a weak vinculum connecting the tendons of *per. d. III* and *pp. d. III*. *M. flex. per. d. III* supplies digit III and the tendon of insertion terminates on the posterior

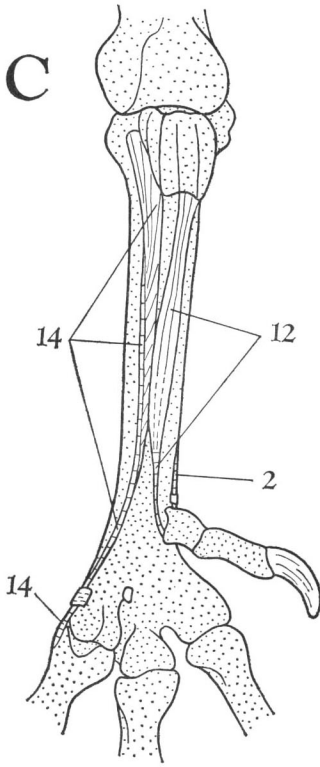


Fig. 4 (on pp. 130–131). Comparison of deepest muscles, posterior view of left foot. — A, *Gallus gallus* (domestic); B, *Perdix dauuricae*; C, *Tetraogallus tibetanus*. See Fig. 3 for explanation.

surface of the base of phalanx 3. It is perforated by the tendon of pp. d. III distal to the tarsometatarsal joint.

The main portion (medial head) of per. d. III has a unipinnate fiber arrangement (except some fibers at the proximal end), with the aponeurosis of origin lying on the anterolateral (deep) side and the tendon of insertion on the other side of the muscle. A short branch of the tendon of insertion extends along the lateral edge of the lateral head. The fibers of the lateral head is divided, and the medial fibers insert on the main tendon and the lateral ones on the lateral branch of the main tendon of insertion.

10) *M. flexor perforatus digiti II* (*M. flex. per. d. II*)

This flat muscle is situated anterior (deep) to *M. flex. per. d. III* and *IV* and posterior to *M. flex. hal. I* on the posterior side of the shank. It has two heads of origin and a distal slip of the belly. The medial head has its origin from the lateral side of the aponeurosis of origin for per. d. III and *IV* (medial heads). The short lateral head arises from the medial side of the aponeurosis of origin for the lateral head of per. d. *IV*. The distal slip takes an origin from the anterior (deep) surface of the aponeurosis that receives the ambiens tendon. This part is inseparable from the distal slip of per. d. *IV* arising from the opposite (posterior) surface of the same aponeurosis. The

tendon of per. d. II passes through its own canal in the tibial cartilage. It is perforated by the tendon of pp. d. II distal to the tarsometatarsal joint and supplies digit II as in per. d. III.

This muscle has a bipinnate fiber arrangement with the tendon of insertion extending along the anterior side of the muscle. The medial fibers consist of those from the medial head and its aponeurosis, whereas the lateral fibers are those of the lateral head and the distal slip. The three perforatus muscles extend the tarsometatarsus and flex digits II, III and IV. They probably work more or less simultaneously. The largest and most powerful of those is per. d. IV, per. d. II being smallest and containing the least number of fibers.

11) *M. flexor hallucis longus (M. flex. hal. l.)*

This long, slender muscle extends from the distal end of the femur down to the base of the hallux. It takes its aponeurotic origin from the popliteal fossa of the femur. The aponeurosis of origin is confluent with that for the medial heads of the perforatus muscles proximally. The belly of *M. flex. hal. l.* lies posterior (superficial) to *M. flex. dig. l.* and anterior to *M. flex. per. d. II.* The stout, flat tendon of insertion passes the posterior end of the tibial cartilage and is situated in a groove on the lateral side of the hypotarsal crest at the proximal end of the tarsometatarsus. The tendon then extends obliquely from the lateral to the medial side, crossing over the tendon of *M. flex. dig. l.* at the middle of the tarsometatarsus to insert on the phalanx of digit I. At the crossing point of the two tendons, *M. flex. hal. l.* lies superficial to *M. flex. dig. l.* and the two are connected by a loose vinculum. At the insertion on the phalanx the tendon perforates the fibrous sheath covering the tarsometatarsal joint and it ends on the base of the claw of the hallux.

The *M. flexor hallucis longus* is a unipinnate muscle. The flat belly extends about half way down the tibiotarsus. The aponeurosis of origin lies on the anterior surface of the belly and the tendon of insertion covers almost the entire posterior surface as a well developed aponeurosis. The fibers arise from the posterior surface of the former and insert on the anterior (inner) surface of the latter. This muscle extends the tarsometatarsus and flexes the hallux. Because of the connection with *M. flex. dig. l.* by vinculum, it can flex all the toes. However, the looseness of the vinculum appears to allow a slight degree of independent action of this muscle, and the flexion of the front toes may not actually occur without simultaneous action of *M. flex. dig. l.*

12) *M. flexor hallucis brevis (M. flex. hal. brev.)*

This muscle runs from the proximal end of the tarsometatarsus to the base of the hallux along the posteromedial side of the bone. Its origin is mainly from the posterior tarsal groove and partly from the posteromedial surface of the tarsometatarsus in its proximal half. The tendon of insertion is very slender in the middle of the tarsometatarsus, but becomes broader distally and ends in a fibrous sheath covering the tarsometatarsal joint and the base of the phalanx of the hallux. This sheath is

perforated by the tendon of *M. flex. hal. I.*

This muscle is a unipinnate one with its fibers inserting on the tendon of insertion covering the posteromedial surface of the muscle. At the proximal end of the muscle the fibers are longer and they insert on the tendon of insertion bipinnately. The action of this muscle is to assist flexing the hallux.

13) *M. flexor digitorum longus (M. flex. dig. I.)*

This very large muscle is situated deepest on the posterolateral side of the shank. It takes a fleshy origin from the posterior and lateral surfaces of the fibula and from the proximal three-fourths of the posterior surface of the tibiotarsus distal to the origin of *M. popliteus*. Fibers also arise from a broad aponeurosis attaching to the lateral side of the fibula at the fibular-tibial joint. The proximal head of the muscle is notched by the stout tendon of *M. biceps femoris*, forming two small distinct heads. The belly terminates on a stout, flat tendon of insertion that passes the deepest bony canal in the hypotarsus. At the level of digit I the tendon trifurcates into three branches. These branches of tendon perforate the tendons of *M. flex. pp. d. II*, *pp. d. III*, and *M. flex. per. d. IV* and extend along the posterior surfaces of digits II, III and IV respectively, each ending on the base of a claw. They send off small branches that attach on the proximal phalanges.

The fibers of this muscle have a bipinnate arrangement. The tendon of insertion extends along the posterolateral surface of the muscle nearly to the base of the medial (main) head. Proximally the medial fibers arise from the posterior surface of the fibula and from the tibiotarsus, whereas the lateral fibers originate from the lateral side of the fibula and the aponeurosis covering the anteromedial surface of the belly. Distally all fibers insert onto the tendon of insertion bipinnately from the surface of the tibiotarsus. This is an extensor of the tarsometatarsus and the most powerful flexor of the three front toes. The tendon is connected to that of *M. flex. hal. I.* by a vinculum extending from the latter tendon. The vinculum is loose and rather weak, but in some specimens the two tendons are attached closely for a long distance in the proximal part of the tarsometatarsus.

14) *M. abductor digiti IV (M. abd. dig. IV)*

This slender muscle lies along the posterolateral side of the tarsometatarsus lateral to *M. flex. hal. I.*, and extends from the proximal end of the bone to phalanx 1 of digit IV. Its origin is fleshy from the lateral side of the hypotarsal crest and from a narrow line on the posterolateral surface of the tarsometatarsus in its proximal half. The muscle inserts by a narrow, flat tendon onto the lateral side of phalanx 1 (of digit IV) at its proximal end. The tendon of insertion covers a greater part of the posterolateral surface of the belly as an aponeurosis, and fibers insert unipinnately onto it. At the very proximal end of origin the fibers have a bipinnate arrangement. This muscle rotates the fourth toe laterad; it may also act to extend phalanx 1 slightly.

15) *M. adductor digiti II* (*M. add. dig. II*)

This muscle is absent in all the specimens that I have dissected.

Comparative Remarks. My dissection of the legs of *Tetrastes*, *Alectornis*, *Perdix*, *Coturnix*, and *Gallus* confirms the general accuracy of the descriptions by HUDSON *et al.* (1959). However, it must be pointed out that, apart from the absence of *M. adductor digiti II*, *Tetraogallus* is much closer to *Tetrastes* (Tetraonidae) than to *Gallus* (Phasianidae) in both shape (relative development) and fiber arrangement of the toe extensors and flexors (and also the pelvic muscles in general). *Gallus* has a relatively stouter, shorter tarsometatarsus and a longer hallux, and all the extensors and flexors are more powerful muscles, each muscle having a larger number of fibers with better developed bellies and/or aponeuroses. In *Alectornis*, *Perdix*, and *Coturnix* the muscle condition is intermediate between *Gallus* and *Tetraogallus* (or *Tetrastes*). These three genera have a slender *M. adductor digiti II*.

Discussion

HUDSON *et al.* (1959) attributes a great taxonomic value to *M. adductor digiti II*, which is present in all galliform birds they examined except the Tetraonidae. They also suggest that a "well developed" *M. adductor digiti II* in the Phasianidae is a primitive condition and that its absence in the Tetraonidae to be a specialization which is an adaptation to extreme cold. The absence of this muscle in *Tetraogallus*, an unquestioned member of the Phasianidae, reduces the value of this feature as a diagnostic character for the families of the Galliformes. *M. adductor digiti II* is absent in many avian families; in the Cuculidae it is present in some genera and absent in others (GEORGE & BERGER, 1966, p. 457; HUDSON, 1937, p. 57). It seems to be a character which is easily modified by functional demand. Further examination of allies of *Tetraogallus* such as *Lerwa* and *Tetraophasis* would be most desirable.

Absence of the muscle in the Tetraonidae and *Tetraogallus* represents very probably a pseudohomologue. Pseudohomology is the independent (not strictly homologous) appearance of the same or very similar features in a morphologically uniform group. The basis of pseudohomology is a similar genetic make-up and developmental potential in related forms. To use BOCK's (1963) term, the members of a morphologically uniform group would possess a high degree of evolutionary homodynamy, thus facilitating independent origins of extremely similar features (see BOCK, 1963, 1967, 1974 for discussion on homology and pseudohomology). When *M. adductor digiti II* in the Tetraonidae and one in the Phasianidae are really pseudohomologous, then the variation of this character in the two families has no taxonomic significance at the family level. Pseudohomologous characters cannot be distinguished from true homologous ones without establishing phylogeny of the group from various taxonomic evidences. Unfortunately, one can never ascertain, with complete certainty, the phylogeny of any group and thus are never certain when features are pseudohomo-

logous rather than homologous.

Contraction and shortening of *M. adductor digiti II* pulls the second toe medially. The function of this muscle in the actual use of the foot is, however, unknown. My observation of captive birds reveals no significant difference in the movement of the toes between pheasants and the Hazel Grouse. Hence, the adaptive significance and phylogenetic sequence of the loss of this muscle cannot be ascertained at this time. The presence or absence of the muscle in gallinaceous birds may be under the influence of a simple selection force, and speed of running is probably the responsible one since toes are flexed as the foot is raised from the ground. I cannot envision any significant functional reasons for concluding that the loss of this muscle is an adaptive modification to extreme cold.

There is little doubt that the Tetraonidae is a homogeneous group and that they are most closely related to the Phasianidae. The taxonomic rank to be given them is largely a matter of personal taste and convenience. I prefer treating the Tetraonidae and the Meleagrididae as subfamilies of the Phasianidae without recognizing further subfamilies in the Phasianoidea in the sense of HUDSON *et al.* (1966, p. 18).

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