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Homology and Evolution of the Deep Dorsal Thigh Musculature in Birds and Other Reptilia

TIMOTHY ROWE
Department of Geological Sciences, University of Texas, Austin, Texas 78713

ABSTRACT Data from adult birds, crocodilians, *Sphenodon*, squamates, turtles, and from the chick embryo are compared to test conflicting hypotheses of homology of the deep dorsal thigh muscles of birds and other reptiles. This comparison suggests that: 1) avian Mm. iliofemoralis externus and iliotrochantericus caudalis (herein renamed "iliofemoralis cranialis") are homologous with M. iliofemoralis of other reptiles; 2) avian Mm. iliotrochanterici cranialis and medius are homologous with one of two divisions of M. pubo-ischio-femoralis internus found in other reptiles (pars dorsalis of Crocodylia); 3) avian M. iliofemoralis internus (herein renamed "cuppedicus") is homologous with the other division of M. pubo-ischio-femoralis internus (pars medialis of Crocodylia). This hypothesis implies a minimum of seven transformations in the number of muscles and their positions of origin and insertion in the evolution of Aves, five of which are recapitulated during ontogeny of the chick. The traditional recognition of three muscles in the "iliotrochantericus group" is topographically accurate, but it is a misnomer and has been a source of misdirection when these muscles are studied in a phylogenetic context. Variations within Aves in the presence of the iliotrochantericus muscles (cranialis or medius) and the iliofemoralis muscles (externus or cranialis) are results of heterochronic perturbations of a conserved developmental program. Unlike most previous interpretations, this view of homology suggests that the evolution of avian bipedality was accompanied by few myological transformations, despite profound modification of the skeleton.

The homologies of the deep dorsal thigh muscles of birds with those of other amniotes have been among the most problematic in avian myology (George and Berger, '66; Vanden Berge, '79). This is in part a reflection of the large transformation that occurred in the hip. Avian evolution involved a shift from the quadrupedal locomotion of primitive archosaurs to the bipedal stance of birds, during which the skeleton of the pelvis and hindlimb were transformed until even the most primitive living birds are markedly different from other living reptiles. Conflicting opinions on these homologies occur in the literature, reflecting different opinions on avian phylogeny and, more fundamentally, different criteria used to test homology. From these accounts (Gadow, 1880, 1882; Gadow and Selenka, 1891; Romer, '23a, '27a,b, '42; Walker, '77; Lance Jones, '79), historic transformation of the avian deep dorsal thigh musculature appears to have been extremely complex, involving possible loss of primitive muscles, evolution of new muscles, reappearance of lost muscles, fusion of muscles, and changes in their innervation and action. However, disagreement exists on precisely which of these transformations are most likely to have occurred. This controversy is further manifested in disagreement on the identity and distribution of some of these muscles within Aves. The problem is complicated by a nomenclature in which a large number of names has been applied with varying usage to a much smaller number of anatomical structures (Table 1).

One source of conflict is that different anatomists have chosen different amniote taxa for their comparisons with birds, and they disagree on which taxon is most informative in studying avian history. Supporting evi-

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Timothy Rowe is now at the Department of Geological Sciences, University of Texas, Austin, TX 78713.

dence for most of the various hypotheses of homology has come from Crocodylia and Squamata, with the latter usually being considered the more informative of the two groups. Romer ('23a), for example, compared birds with crocodilians but reached only an admittedly tentative conclusion regarding the homologies of avian deep thigh muscles in non-avian amniotes. He was unable to resolve his uncertainty even after studying development of the thigh muscles of the chick, finding that "the embryological evidence is . . . inconclusive" (Romer, '27a, p. 375). Later, however, after studying development of the thigh in the squamate *Lacerta*, Romer changed his opinion without reservation to favor a different view of the avian homologies, citing what he considered to be conclusive evidence (Romer, '42). Walker ('77) agreed at length with Romer's second opinion and promoted additional corroborative arguments based on squamate characters. Others have chosen to compare birds either with adult mammals (Howell, '38), or with mammalian ontogenetic stages (Lance Jones, '79).

Compelling evidence has long existed that Aves shares a more recent common ancestry with Crocodylia than with any other living taxon, that Squamata is a more distant relative, and that Chelonia and Mammalia are even more remotely related (Fig. 1; e.g., Gaffney, '80; Gauthier, '84; Gauthier et al., in press). Consequently, estimates of the relevance of squamate characters to this issue may be mistaken, because any homologous characters shared by Aves and Squamata could have evolved no more recently than in their most recent common ancestor, i.e., the most recent common ancestor of Sauria (*sensu* Gauthier, '84: *Sphenodon* + Squamata + Crocodylia + Aves). Hence, comparisons of birds with squamates or mammals are informative with respect to the more distant history of birds, but not on the evolution of archosaurian or uniquely avian characters.

In this study I reexamine the homology of deep thigh muscles in birds by employing the hypothesis that Aves and Crocodylia are sister groups comprising Archosauria, and that Lepidosauria, Chelonia, and Mammalia are its consecutively more distant outgroups (Fig. 1). I also examine the development and distribution of deep thigh muscles within Aves. This comparison supports a different hypothesis of avian thigh muscle homology from that currently accepted by most students.

TABLE 1. Synonymy of avian deep thigh muscles

Gadow and Selenka (1891)	Hudson ('37)	Howell ('38)	Fisher ('46)	George and Berger ('66)	Vanden Berge ('79)	Recommended here
Iliotrochantericus anterior	Iliotrochantericus anterior	Iliacus	Iliacus	Iliotrochantericus anterior	Iliotrochantericus cranialis	Iliotrochantericus cranialis
Iliotrochantericus medius	Iliotrochantericus medius	—	Iliotrochantericus medius	Iliotrochantericus medius	Iliotrochantericus medius	Iliotrochantericus medius
Iliotrochantericus posterior	Iliotrochantericus posterior	Gluteus profundus	Gluteus profundus	Iliotrochantericus posterior	Iliotrochantericus caudalis	Iliofemoralis cranialis
Iliofemoralis externus	Gluteus medius et minimus	Piriformis	Piriformis	Gluteus medius et minimus	Iliofemoralis externus	Iliofemoralis externus
Iliofemoralis internus	Iliacus	Psoas	Psoas	Iliacus	Iliofemoralis internus	Cuppedicus

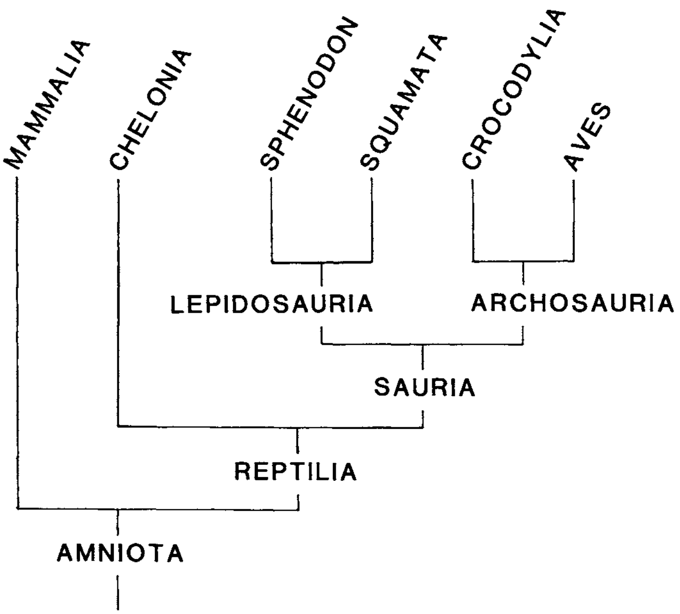

Fig. 1. Phylogeny of higher systematic categories of Amniota employed in this study (from Gauthier, '84; Gauthier et al., in press).

Phylogeny of the avian deep dorsal thigh musculature appears to be far less complex than generally believed, and despite many skeletal differences, birds and crocodilians share unique myological similarities. Moreover, most of the phylogenetic transformations implied by this hypothesis are recapitulated in avian ontogeny.

MATERIALS AND METHODS

In order to confirm attributes of muscles described in published accounts, I dissected the deep thigh muscles in adult and subadult specimens of a number of avian species, and in a young (22-cm snout-vent length) caiman. All materials dissected are from the spirit collections of the Departments of Ornithology and Herpetology, National Museum of Natural History, with the exception of a number of young (6 to 10 weeks) anatids, meleagridids, tetraonids, and phasianids obtained from markets in Washington, D.C. I have relied on published accounts for details of the myology of *Sphenodon*, (Gadow, 1882; Osawa, 1898; Byerly '25) Chelonia (Gadow, 1882; Zug, '71; Walker, '73) and *Lacerta* (Gadow, 1882; Romer, '42). Skeletons of these taxa in the National Museum of Natural History and University of California (Berkeley) Museum of Paleontology were also examined, to confirm positions of scars of attachment of the muscles under study.

The methods employed in this study are essentially the phylogenetic methods discussed by Wiley ('81), Raikow ('82) and Gauthier (in press). However, I follow the suggestion of Maddison et al. ('84) of employing at least two consecutive outgroups to determine polarity of character transformation. Using these methods, for example, I view character states shared uniquely by birds and crocodilians, based on comparisons with Lepidosauria and Chelonia, as derived states that distinguish Archosauria among reptiles.

RESULTS

Introduction to the problem

The avian muscles that have been the focus of controversy are derivatives of the embryonic deep dorsal mass of the thigh, which during development divides to produce up to five separate adult muscles (Romer, '27a). Under current nomenclature (Vanden Berge, '79) these are Mm. iliofemoralis externus, iliofemoralis internus, and the three muscles of the iliotrochantericus group, Mm. iliotro-

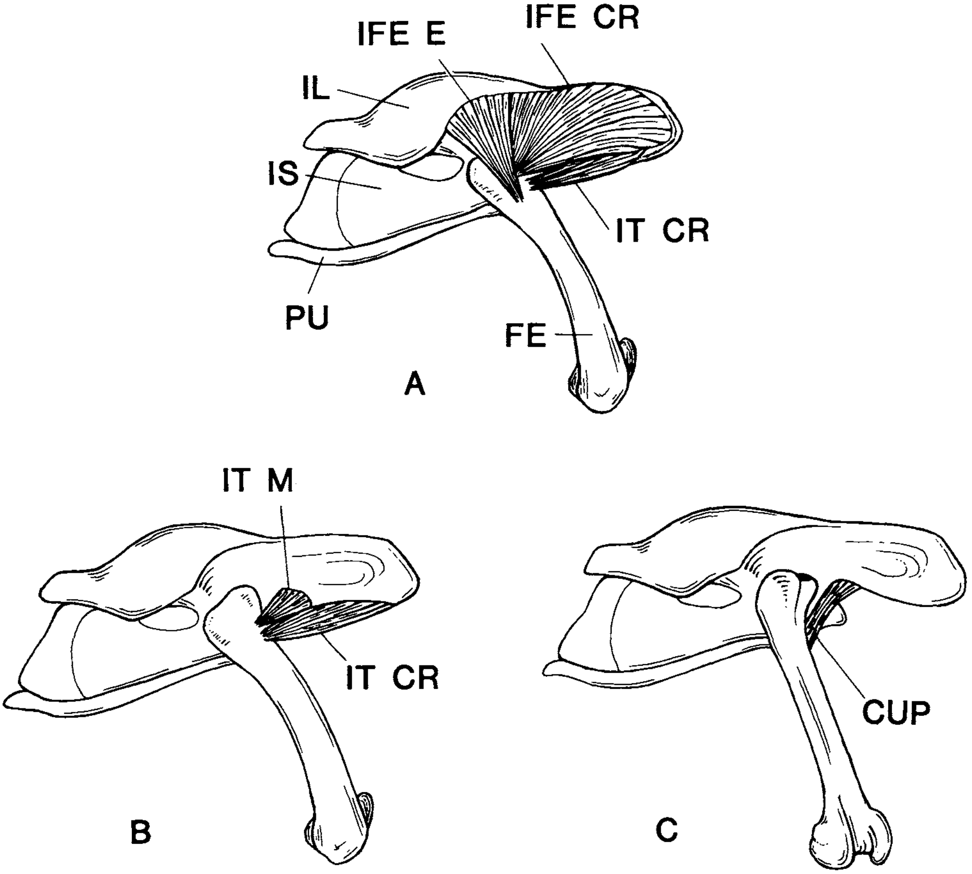

Fig. 2. *Gallus.* Lateral view of right pelvis and femur of 8-week old chicken, showing only those muscles that differentiate from the embryonic deep dorsal mass. A) Superficial view. B) The Mm. iliofemoralis externus and iliofemoralis cranialis (=iliotrochantericus caudalis) have been removed. C) Iliofemoralis and iliotrochantericus muscles have been removed, and knee has been twisted outwards to show more clearly M. cuppedicus. CUP, cuppedicus (=iliofemoralis internus); FE, femur; IFE CR, iliofemoralis cranialis (=iliotrochantericus caudalis); IFE E, iliofemoralis externus; IL, ilium; IS, ischium; IT CR, iliotrochantericus cranialis; IT M, iliotrochantericus medius; PU, pubis.

chanterici cranialis, medius, and caudalis (Fig. 2). Only two muscles in non-avian Reptilia have been regarded as in any way homologous with the five bird muscles, namely Mm. iliofemoralis and pubo-ischio-femoralis internus [PIFI] (Gadow, 1882; Gadow and Selenka, 1891; Romer, '23a, '27a, '27b, '42; Walker, '77; Lance Jones, '79). In *Sphenodon* (Osawa, 1898), Squamata (Romer, '42), Chelonia (Zug, '71; Walker, '73; see below) and Crocodylia (Romer, '23a), M. iliofemoralis is a single muscle, while M. PIFI is divided into two bellies (Fig. 3). In some squamates, M. PIFI is divided into three bellies, but this is a condition unique to squamates (Romer, '42). Hence, the condition from which birds evolved was one in which M. iliofemoralis was a single muscle, and M. PIFI was divided into two parts.

Descriptions of the differentiation of the thigh musculature in crocodilians, *Sphenodon*, and turtles are not currently available, so reptilian ontogenetic patterns can not yet be compared. However, comparison of their adult attributes with those in birds does provide evidence for a minimum number of transformations in avian phylogeny, and the occurrence of these same transformations in

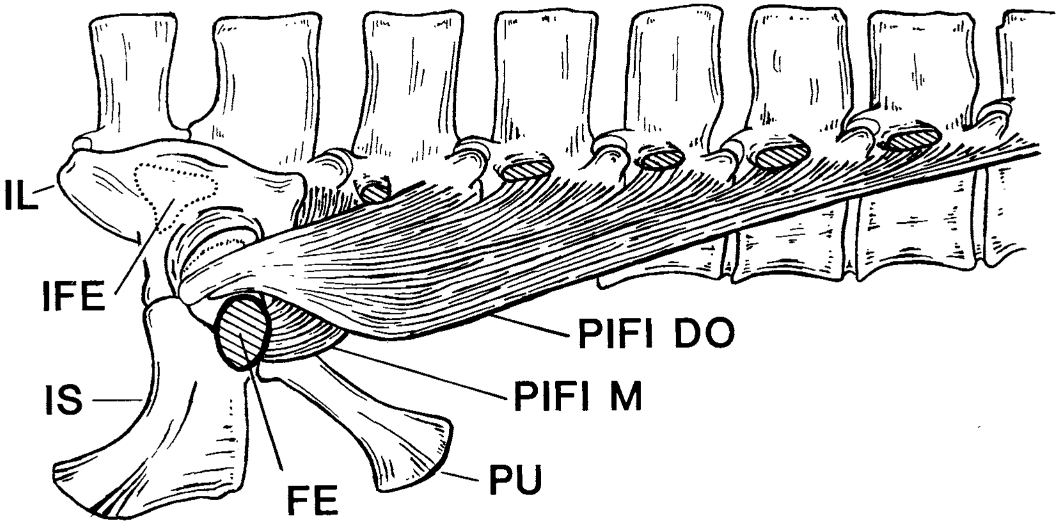

Fig. 3. *Alligator*. Right lateral view of pelvis and femur showing deep dorsal thigh muscles. The M. iliofemoralis has been removed; its position of origin on the lateral face of the ilium is indicated by the dotted line. The femur has been cut across the shaft, its distal half removed, and the cut surface indicated by cross hatching (after Romer, '23a). FE, femur; IFE, position of origin of iliofemoralis; IL, ilium; IS, ischium; PIFI DO, pubo-ischio-femoralis internus pars dorsalis; PIFI M, pubo-ischio-femoralis internus pars medialis; PU, pubis.

avian ontogeny provides independent corroboration that they occurred historically (Nelson, '78; Fink, '82; DeQueiroz, '85; Kluge, '85).

Although there is general agreement that these muscles share some kind of homological relationship, previous investigators disagree on precisely what that relationship is and imply different sets of historic transformations (Gadow, 1880, 1882; Gadow and Selenka, 1891; Romer, '23a,b, '42; Walker, '77; Lance Jones, '79). These different hypotheses may be evaluated by comparison with an estimate of the minimum number and kinds of transformations that must have occurred historically. This estimate is made below by comparing adult muscles in Aves with those of other Reptilia. Historical transformations suggested by this comparison are then compared to ontogenetic transformations occurring during early development of the chick.

Deep dorsal thigh muscles in adult Reptilia

Chelonia

In both pleurodire and cryptodire turtles, M. iliofemoralis is a single muscle that arises from the dorsolateral surface of the ilium, just dorsal to the acetabulum (Fig. 4). It may also expand craniad onto one or two presacral vertebrae and onto adjacent parts of the carapace, in a condition unique to turtles. It inserts on the dorsal surface of the femoral trochanter majoris and acts to abduct and protract the femur (Zug, '71; Walker, '73). In Trionychidae, M. iliofemoralis divides to form two heads with a common insertion, in a condition unique to this family (Zug, '71). As in other Reptilia and Lissamphibia, but not mammals, the chelonian iliofemoralis is innervated by branches of both the femoral and peroneal nerves (Gadow, 1882).

The chelonian M. PIFI is divided into two parts. These are referred to as the anteroventral division and the posterodorsal division (Zug, '71; Walker, '73). In all turtles the anteroventral division is a large and powerful muscle that originates from the dorsal surface of the pubis and epipubic cartilage. In cheloniids the anteroventral division may be divided into separate superficial and deep layers, and in pleurodires its origin may expand onto the plastron, but both of these conditions are derived within Chelonia (Walker, '73). The posterodorsal division originates from one or more presacral vertebrae and costal plates and from the medial surface of the ilium. The two divisions pass together in front of the acetabulum to insert as a

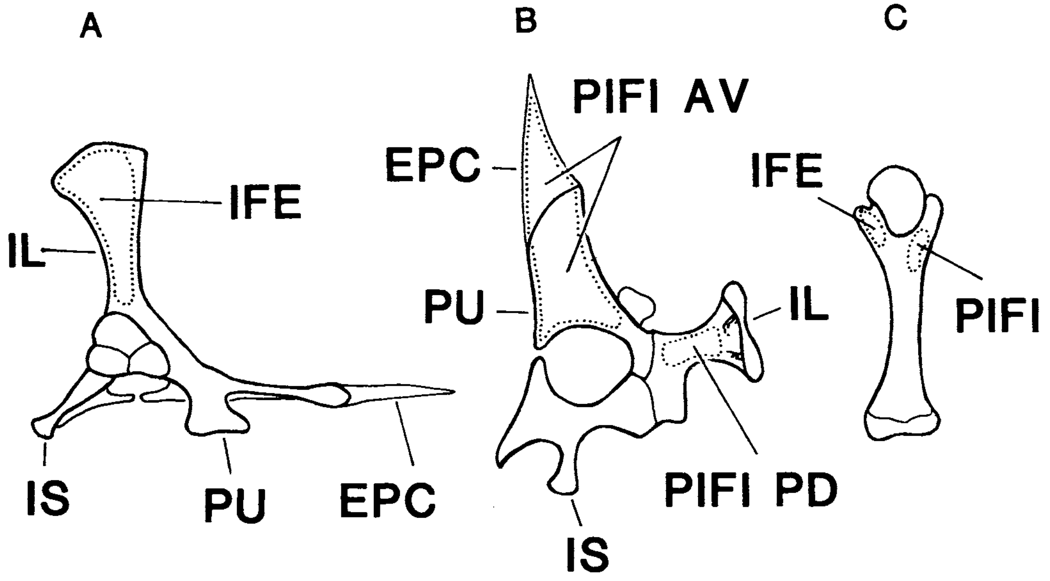

Fig. 4. *Pseudemys*. Origins and insertions of deep dorsal thigh muscles on pelvis and femur. A) Right lateral view of pelvis. B) Dorsomedial view of pelvis. C) Right femur in dorsal view (after Walker, '73; Zug, '71). EPC, epipubic cartilage; IFE, iliofemoralis; IL, ilium; IS, ischium; PIFI, common insertion of anteroventral and posterodorsal divisions of pubo-ischio-femoralis internus; PIFI AV, origin of anteroventral division of pubo-ischio-femoralis internus; PIFI PD, origin of posterodorsal division of pubo-ischio-femoralis internus; PU, pubis.

common tendon on the dorsal surface of the femoral shaft and trochanter minoris. As in other Reptilia, both divisions of M. PIFI are innervated by branches of the femoral nerve (Gadow, 1882).

Turtles are like birds but unlike other reptiles in that the insertions of both Mm. iliofemoralis and PIFI are on the proximal end of the femur rather than on the shaft. However, when all of the character data pertinent to reptilian relationships are taken into account (e.g., Gauthier et al., in press), it is most parsimonious to conclude that this condition evolved independently in turtles and birds.

Lepidosauria

As in turtles, M. iliofemoralis in the lepidosaurs *Sphenodon* (Osawa, 1898; Byerly, '25) and Squamata (Romer, '42) arises from the lateral face of the ilium, immediately dorsal to the acetabulum (Fig. 5). It inserts on the caudal surface of the middle third of the femoral shaft and abducts and rotates the femur forward. It receives dual innervation, from branches of the femoral and peroneal nerves.

As in turtles, the M. PIFI in *Sphenodon* and Squamata arises from the dorsal or inner surface of the pubo-ischiadic plate. It is a large muscle that covers most of the dorsal surface of the pubis and cranial half of the ischium. Byerly ('25) reported that M. PIFI is undivided in *Sphenodon*; however, Osawa (1898), using the name pubo-ischio-trochantericus internus, described and illustrated a separate small cranial division. Both divisions pass in front of the pubis, lateral to the pubic tuberosity, to insert on the dorsal surface of the middle third of the femoral shaft. In some squamates (e.g., *Lacerta*), M. PIFI is divided into three parts, pars dorsalis, medialis, and ventralis (synonymous with M. PIFI parts I, II, and III, respectively, of Romer, '42). All three divisions protract and rotate the femur forward. The squamate M. PIFI ventralis corresponds to the small cranial division in *Sphenodon*, while the caudal division in *Sphenodon* is itself divided in some squamates to form Mm. PIFI dorsalis and medialis. Based on positional criteria, the anteroventral division of M. PIFI in turtles is homologous with the large caudal division in *Sphenodon* and the undivided anlage of

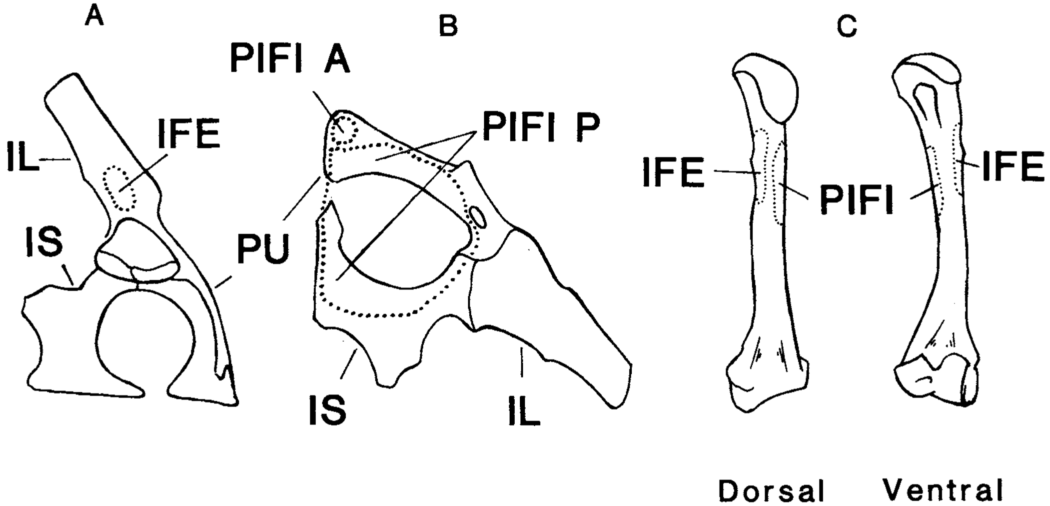

Fig. 5. *Sphenodon*. Origins and insertions of deep dorsal thigh muscles on pelvis and femur (after Gadow, 1882; Osawa, 1898). A) Right lateral view of pelvis. B) Dorsomedial view of pelvis. C) Right femur. IFE, iliofemoralis; IL, ilium; IS, ischium; PIFI, common insertion of anterior and posterior divisions of pubo-ischio-femoralis internus; PIFI A, origin of anterior division of M. pubo-ischio-femoralis internus; PIFI P, origin of posterior division of M. pubo-ischio-femoralis internus; PU, pubis.

Mm. PIFI dorsalis and medius in squamates. The posterodorsal division of turtles is homologous with the M. PIFI ventralis of squamates and the small cranial division of M. PIFI in *Sphenodon* (Table 2; Walker, '73).

Crocodylia

In crocodilians, as in turtles and lepidosaurs, M. iliofemoralis arises from a large part of the lateral face of the ilium, immediately dorsal to the acetabulum (Fig. 3). In Archosauria, the ilium is antero-posteriorly expanded over the condition in other reptiles and the muscles arising from the ilium are correspondingly enlarged. The area of origin of M. iliofemoralis in both crocodilians and birds is thus expanded, with its rear edge extending well caudal to the rear margin of the acetabulum. This muscle inserts along the caudal edge of the femoral shaft, well distal to the femoral head, between the two heads of M. femorotibialis (Fig. 6). It receives dual innervation, from branches of the femoral nerve of the crural plexus, and the peroneal nerve of the lumbar plexus (Gadow, 1882; Romer, '23a). From its position, M. iliofemoralis evidently serves to abduct and rotate the femur forward.

As in turtles and lepidosaurs, the crocodilian M. PIFI is considerably larger than M. iliofemoralis. It is divided into two parts, pars dorsalis and pars medialis (PIFI parts II and I, respectively, of Romer, '23a), having different origins and insertions. Unlike turtles and lepidosaurs, in which M. PIFI arises from the pubo-ischiadic plate, in crocodilians it arises from beneath the vertebral column. Pars dorsalis lies entirely cranial to the acetabulum, where it originates ventrally on the six presacral transverse processes. It splits distally to insert in two separate points on the dorsal and cranial surfaces of the femoral shaft, well distal to the femoral head. Pars medialis originates from the medial surface of the ilium and ventral surfaces of the sacral ribs. It passes around the front of the ilium to insert distal to the insertion of pars dorsalis, on the caudal surface of the femur. Its area of origin and belly lie medial to the belly of pars dorsalis. Both divisions serve to abduct the femur and rotate it upward, forward, and inward. As in other Reptilia, both parts of M. PIFI receive innervation from only the femoral nerve (Gadow, 1882; Romer, '23a). The crocodilian M. PIFI medialis is homologous with the anteroventral division of M. PIFI in Chelonia, the posterior division in *Spheno-*

don, and the undivided anlage of Mm. PIFI dorsalis and medius in Squamata (Walker, '73). The crocodilian M. PIFI dorsalis is homologous with the posterodorsal division of Chelonia, the pars ventralis of Squamata, and the cranial division in *Sphenodon* (Table 2).

Aves

In birds, the ilium and sacrum are greatly expanded to either side of the acetabulum compared with the condition found in nondinosaurian Reptilia (Romer, '23b). The ala preacetabularis of the ilium is expanded forward over what is the lumbar region of other Reptilia. As a result, the lumbar plexus in birds issues from between vertebrae that have become incorporated into the sacrum, and the ilium completely covers the area from which M. PIFI arises in crocodilians. The musculature originating from the lateral face of the ilium is correspondingly expanded. Unlike the condition of other Reptilia, there are up to five separate muscles in birds, all of which arise solely from the ilium.

The M. iliotrochantericus cranialis is reported to be present in all birds (George and Berger, '66; but see below), where it originates on the ventrolateral edge of the ilium, entirely cranial to the acetabulum (Fig. 2), and inserts on the trochanter femoris (Fig. 7). It rotates the femur forward and inward, and is innervated by a branch of the femoral nerve (Romer, '27a; George and Berger, '66).

The M. iliotrochantericus medius is reported to be present in most but not all birds (see below). It originates from the ventrolateral edge of the ilium, cranial to the acetabulum, and just caudal to the origin of iliotrochantericus cranialis. It inserts on the trochanter femoris. It performs the same action and has the same innervation as M. iliotrochantericus cranialis. When present, it may have an incompletely divided origin or a common tendon of insertion with M. iliotrochantericus cranialis.

The muscle currently referred to as iliotrochantericus caudalis (e.g., Vanden Berge, '79; renamed below "iliofemoralis cranialis") is reportedly present in all birds (George and Berger, '66; but see below). It is quite large, taking broad origin from the fossa iliaca dorsalis of the large ala preacetabularis of the ilium. Its area of origin lies adjacent to the acetabulum. The fibers of M. iliotrochantericus caudalis pass ventrolaterally and converge toward their point of insertion on the

TABLE 2. Homologies of deep dorsal thigh muscles in Reptilia

Chelonia	Sphenodon	Squamata	Crocodylia	Aves
PIFI[1] Anteroventral division Posterodorsal division	PIFI Posterior division Anterior division	PIFI Dorsalis (I) Medius (II) Ventralis (III)	PIFI Medialis Dorsalis	Cuppedicus (=iliofemoralis internus) Iliotrochantericus Cranialis Medius
Iliofemoralis	Iliofemoralis	Iliofemoralis	Iliofemoralis	Iliofemoralis Cranialis (=iliotrochantericus caudalis) Externus

[1] PIFI = pubo-ischio-femoralis-internus.

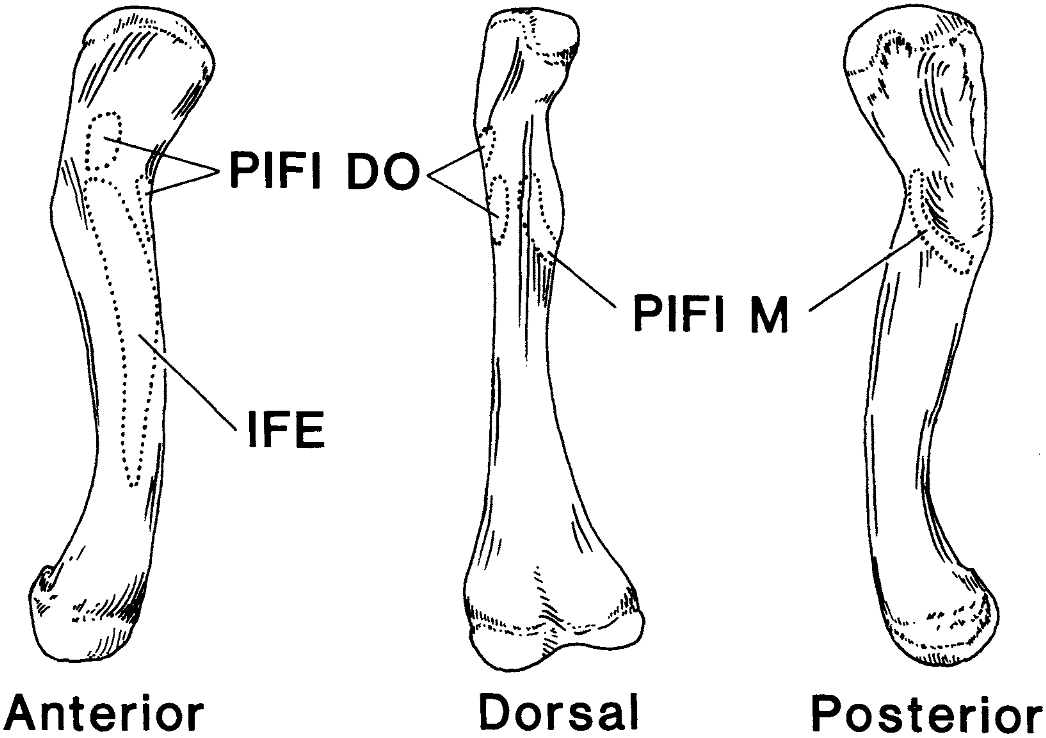

Fig. 6. *Alligator*. Insertions of deep dorsal thigh muscles on left femur (after Romer, '23a). IFE, iliofemoralis; PIFI DO, pubo-ischio-femoralis internus pars dorsalis; PIFI M, pubo-ischio-femoralis internus pars medialis.

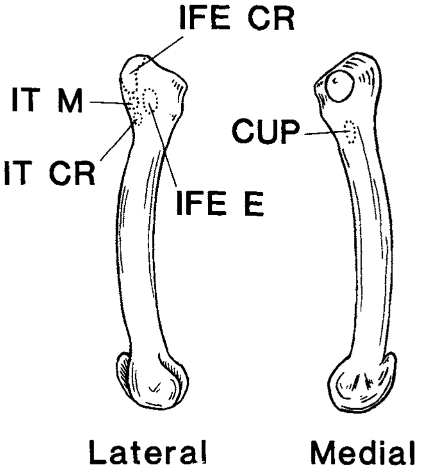

Fig. 7. *Gallus*. Insertions of deep dorsal thigh muscles on left femur. CUP, cuppedicus (=iliofemoralis internus); IFE CR, iliofemoralis cranialis (=iliotrochantericus caudalis); IFE E, iliofemoralis externus; IT CR, iliotrochantericus cranialis; IT M, iliotrochantericus medius.

proximal end of the trochanter femoris. This muscle rotates the femur forward and inward and receives dual innervation, from branches of the femoral and peroneal nerves (Romer, '27a).

The M. iliofemoralis externus also originates from the lateral surface of the ilium immediately dorsal to the acetabulum, and inserts on the trochanter femoris. This muscle is present in many but not all birds (see below). It rotates the femur forward and inward and also receives dual innervation, from branches of the femoral and peroneal nerves.

The muscle currently referred to as iliofemoralis internus (renamed below "cuppedicus") is present in nearly all birds. It is reportedly absent only in "*Tauraco leucotis* (Musophagidae), certain genera of Old World cuckoos (*Coua, Carpococcyx, Centropus, Chrysococcyx, Cuculus*), *Upupa epops, Indicator variegatus,* [and] *Eugenes fulgens*" (George and Berger, '66, p. 418). It arises from the ventral edge of the ilium, immediately cranial to the acetabulum, and deep to the bellies of Mm. iliotrochanterici cranialis and medius. It inserts in the medial surface of the femur, immediately distal to the inturned femoral head. It weakly adducts the femur and rotates it forward and outward, and is innervated by a branch of the femoral nerve.

Comparison of adult Reptilia

Comparison of adult attributes in Aves with those of non-avian Reptilia indicates that at least three kinds of phyletic transformation occurred during the evolution of birds.

1) Increase in the number of muscles. This is suggested because the five avian muscles are represented by only three muscles (M. iliofemoralis and two bellies of M. PIFI) in Crocodylia, *Sphenodon*, and Chelonia. As discussed above, the presence of two heads in M. iliofemoralis of Trionychidae and three divisions of M. PIFI in Squamata are conditions unique to these taxa. During avian history, therefore, a minimum of two additional divisions of the three ancestral muscles must have occurred, to produce the five adult avian muscles. It is conceivable that the additional avian muscles migrated to this region from elsewhere during embryogenesis, but ontogenetic data discussed below refute this possibility.

2) Shifts in the position of muscle insertion. This must have occurred because M. iliofemoralis and all divisions of M. PIFI in Crocodylia and Lepidosauria insert on the femoral shaft well distal to its head, whereas in Aves all five insert more proximally, on or near the trochanter femoris. The proximal insertion of the deep thigh muscles in Chelonia might superficially resemble the avian condition, but this is a convergent development that was not present in the most recent common ancestor that Chelonia shared with Aves (see above). Hence, proximal migration of insertion position occurred at least three times during the evolution of birds. However, this minimum number could occur only if the insertions shifted proximally before the division of the distal ends of the muscles was complete.

3) Shifts in the position of muscle origin. Only one of the muscles under study (M. iliofemoralis) takes origin from the lateral surface of the ilium in Crocodylia, Lepidosauria, and Chelonia, but all five do in birds. This difference requires a minimum of two muscle origin shifts, provided, however, that they occurred before complete division of the muscle origins had occurred.

From this comparison of adults alone, there is no evidence for loss of any ancestral muscles during avian phylogeny. Neither is transformation of innervation or action suggested, because in all Reptilia, including Aves, these muscles receive only femoral and/or peroneal innervation, and they perform similar ranges of action.

Hypotheses of homology

There has been general agreement that the avian M. iliofemoralis externus is homologous with M. iliofemoralis of other Reptilia (Gadow, 1880, 1882; Gadow and Selenka, 1891; Romer, '23a, '27a,b, '42; Walker, '77; Lance Jones, '79). Both have similar position of origin, dual innervation, and perform similar ranges of action. Because in non-avian Sauria M. iliofemoralis inserts on the shaft of the femur well distal to the head, this hypothesis requires that its position of insertion has shifted proximally in birds. This appears likely because proximal migration of its insertion also occurs during early stages in avian ontogeny (see below).

There is also general agreement that avian M. iliofemoralis internus (renamed below "cuppedicus") is homologous with at least part of one of the divisions of M. PIFI of other Reptilia (Gadow, 1880, 1882; Gadow and Selenka, 1891; Romer, '23a, '27a,b, '42; Walker, '77; Lance Jones, '79). This hypothesis requires that during avian history the homolog of M. iliofemoralis internus shifted its insertion proximally, and that its position of origin moved onto the ilium. As described below, the phylogenetic shift of its insertion is recapitulated during avian ontogeny. The hypothesized shift in origin is substantiated only by adult morphology, however, because throughout ontogeny the entire deep dorsal mass takes origin from the lateral surface of the ilium (Romer, 27a).

Despite general agreement on the homology of M. iliofemoralis internus (renamed below "cuppedicus") with part of M. PIFI in other Reptilia, the developmental pathway of iliofemoralis in birds has been controversial. After studying development of the chick, Romer ('27a) believed M. iliofemoralis internus to be a derivative of the embryonic deep dorsal mass. Later, after studying the development of *Lacerta*, he rejected this view (Romer, '42). Based on new ideas about the homologies of the other avian deep thigh muscle, Romer concluded that his earlier observations were erroneous, and that M. iliofemoralis internus must be derived from the superficial dorsal mass, not the deep dorsal mass. Romer's second opinion has been the most generally accepted of the two (e.g., Lance Jones, '79). However, throughout avian ontogeny M. iliofemoralis internus originates from a deep position adjacent to the acetabulum, and its insertion remains on the proximal half of the femur. All of the undisputed deep dorsal mass derivatives also originate from a deep position adjacent to the acetabulum and insert on the proximal half of the femur. Together with M. iliofemoralis internus, they lie caudomedial to the course of the femoral nerve through the thigh. In contrast, derivatives of the superficial dorsal mass originate far from the acetabulum, either from the periphery of the ilium or pubis, or from the shaft of the femur. They insert on the tibia or fibula, not on the femur, and they lie craniolateral to the femoral nerve. Romer's first opinion, that M. iliofemoralis internus develops from the deep dorsal mass, thus appears more accurate.

The homology of the three iliotrochantericus muscles, and whether some part of M. PIFI has been lost in birds, have been the subject of debate. Gadow (1880) and Romer ('23a) concluded from similarities in position that the avian iliotrochantericus group and M. iliofemoralis internus are both homologous with M. PIFI dorsalis of Crocodylia. But later Gadow and Selenka (1891) argued that M. PIFI dorsalis must have been lost in birds, that the iliotrochantericus group is homologous with M. iliofemoralis in Crocodylia, and that M. iliofemoralis internus is the sole remnant of M. PIFI in Aves. Their rationale was that M. PIFI dorsalis receives only femoral innervation and therefore could not be homologous with the iliotrochantericus group, because iliotrochantericus caudalis receives both femoral and peroneal innervation.

Romer ('42) also later changed his opinion to defend the view of Gadow and Selenka (1891), that M. PIFI dorsalis was lost, and that the avian iliotrochantericus group is homologous with M. iliofemoralis of Lepidosauria and Crocodylia. He had already pointed out that in the developing chick Mm. iliotrochantericus caudalis and iliofemoralis externus differentiate from their common anlage relatively late in ontogeny, suggesting to him, admittedly inconclusively, that the iliotrochantericus group was derived from M. iliofemoralis (Romer, '27a, p. 375). He later believed he had confirmation of this derivation in his study on the development of *Lacerta*, arguing that the "iliotrochanterici are derived from the reptilian ilio-femoralis as their development and position posterior to the femoral nerve would suggest," and "in the chick the iliofemoralis internus is the lone survivor of the pubo-ischio-femoralis internus" (Romer, '42, pp. 280–281). This view has been widely accepted (Galton, '69; Walker, '77; Lance Jones, '79; Cooper, '81).

Despite its popularity, this view requires a number of transformations for which there is no corroborative evidence. As argued above, comparison of adult Reptilia provides direct evidence of only two splitting events, three insertion shifts, and two origin shifts in the history of birds. But implicit in the view of Gadow and Selenka (1891) and Romer ('42) are all these plus a number of additional transformations. First, these authors hypothesize the loss of M. PIFI dorsalis. Because the divided M. PIFI of other Reptilia would be represented by a single muscle in Aves, a second transformation is required, an additional splitting event (for a total of three) transforming the undifferentiated M. iliofemoralis into avian Mm. iliofemoralis externus and the three iliotrochanterici. Thirdly, a transformation of action is required because M. iliofemoralis is a strong abductor of the femur, but Mm. iliotrochanterici cranialis and medius perform no abduction, and instead protract the femur and rotate it forwards and inwards. Finally, M. iliofemoralis receives both femoral and peroneal innervation, but two of its hypothesized derivatives, Mm. iliotrochanterici cranialis and medius, receive only femoral innervation. No observations in adults require any of these transformation hypotheses, nor has evidence been found to substantiate them in avian ontogeny.

The source of this problem appears to be the assumption that the three muscles of the iliotrochantericus group together form a natural unit that is uniquely differentiated from a single homologous representative in other Reptilia. All previous students have sought a single homolog for the three avian iliotrochantericus muscles. But the evidence currently available argues for homology of M. iliofemoralis with only M. iliotrochantericus caudalis, not with all three of the iliotrochantericus muscles. Only when this hypothesis is extended to include Mm. iliotrochanterici

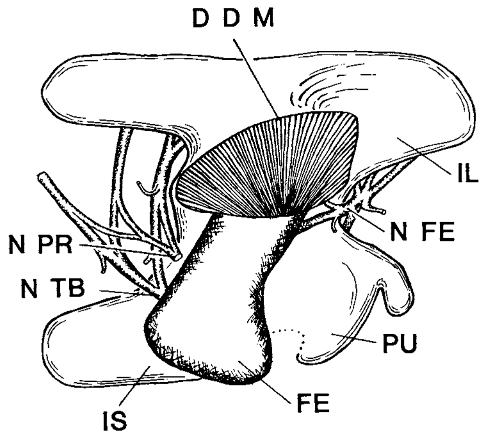

Fig. 8. Pelvic region of embryonic chick early on the sixth day of development. The superficial muscle mass has been removed to show the undifferentiated deep dorsal mass (after Romer, '27a). Drawings of embryos are not to scale. D D M, deep dorsal mass; FE, femur; IL, ilium; IS, ischium; N FE, femoral nerve; N PR, peroneal nerve; N TB, tibial nerve; PU, pubis.

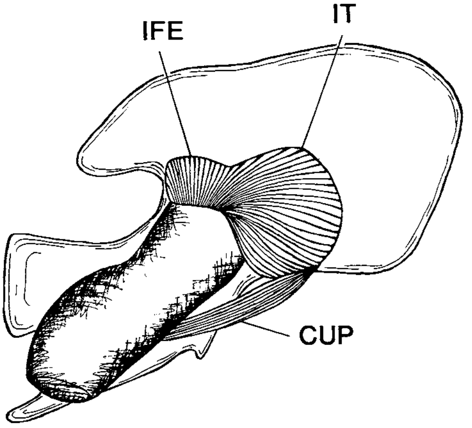

Fig. 9. Deep dorsal thigh musculature of embryonic chick late on the sixth day of incubation (stage III) (after Romer, '27a). CUP, cuppedicus; IFE, iliofemoralis (undifferentiated), IT, iliotrochantericus (undifferentiated).

cranialis and medius must one assume the additional transformations described above.

The most parsimonious hypothesis supported by the characters described above is that avian Mm. iliotrochantericus caudalis (renamed below "iliofemoralis cranialis") and iliofemoralis externus are homologous with M. iliofemoralis in other Reptilia, and that avian Mm. iliotrochanterici cranialis and medius are homologous with the single division of M. PIFI in other Reptilia that is the equivalent of crocodilian M. PIFI dorsalis. As discussed earlier, avian M. iliofemoralis internus (renamed below "cuppedicus") is homologous with the single division of M. PIFI in other Reptilia that is equivalent to the crocodylian M. PIFI pars medialis (Table 2). This hypothesis requires only the seven transformations described above, whereas the competing hypotheses require additional steps. A test of this hypothesis can be found in avian ontogeny. As discussed below, five of the seven inferred phylogenetic transformations are recapitulated.

Development of deep thigh muscles in the chick

The following account is based on Romer's ('27a) study on the ontogeny of the chick. During early ontogeny, myoblastic mesenchyme accumulates in the limb bud and then cleaves in an orderly pattern to produce up to five adult muscles. The first division is a cleavage along a horizontal plane that divides the early myoblastic condensation into dorsal and ventral masses situated on either side of the primordium of the femur. By early on the sixth day of development (Romer's stage II) the dorsal mass has itself divided into separate superficial and deep masses. The deep mass at this stage receives innervation only from a twig of the femoral nerve passing from in front of the acetabulum) (Fig. 8).

By late on the sixth day (Romer's stage III), the deep dorsal mass has begun to differentiate (Fig. 9). A broad cleft at their common origin distinguishes a cranial (preaxial) from a caudal (postaxial) mass. At this stage a twig from the peroneal nerve can be seen passing around the posterior edge of the pelvis to innervate the caudal mass. Cranially, differentiation proceeds more rapidly, and M. iliofemoralis internus (renamed below "cuppedicus") has separated along most of its length but maintains a common origin with the cranial mass. On the sixth day, it inserts on a point about half-way down the femur, but during subsequent developmental stages (Figs. 10, 11) the insertion migrates proximally, until it reaches its adult position immediately distal to the inturned femoral

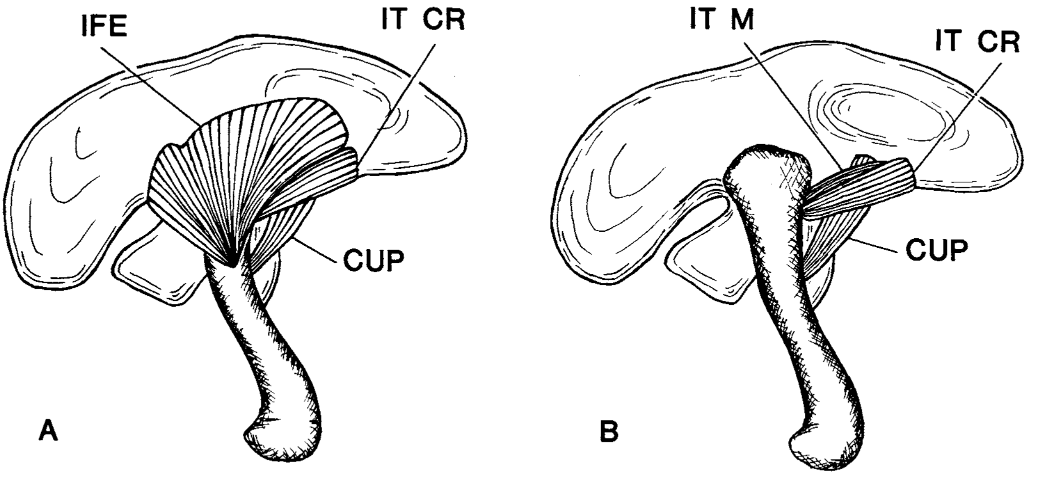

Fig. 10. Deep dorsal thigh musculature of embryonic chick on seventh day (stage IV) (after Romer, '27a). A) Superficial view. B) Iliofemoralis removed. CUP, cuppedicus; IFE, iliofemoralis (undifferentiated); IT CR, iliotrochantericus cranialis; IT M, iliotrochantericus medius.

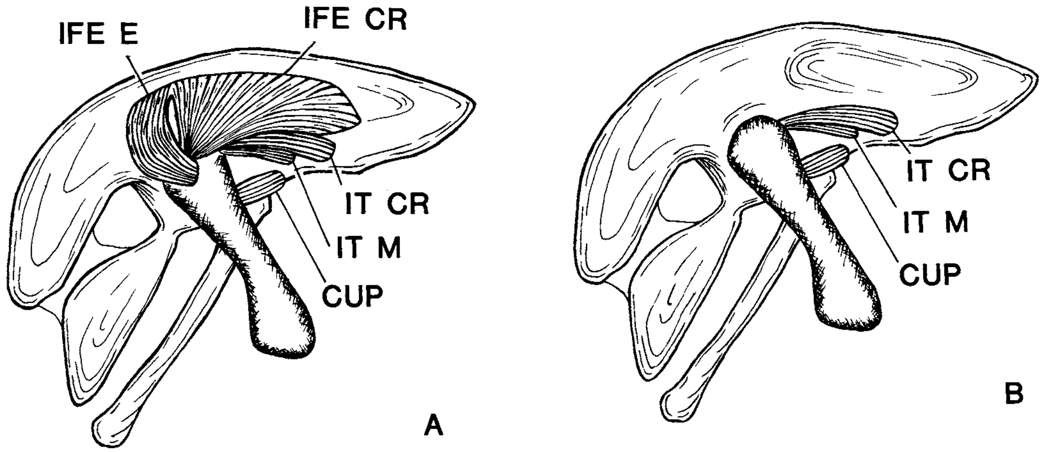

Fig. 11. Deep dorsal thigh musculature of embryonic chick on the eighth day (stage V) (after Romer, '27a). A) Superficial view. B) Iliofemoralis anterior and externus removed. CUP, cuppedicus; IFE CR, iliofemoralis cranialis; IFE E, iliofemoralis externus; IT CR, iliotrochantericus cranialis; IT M, iliotrochantericus medius.

head. By the eighth day, the insertion of M. iliofemoralis internus ("cuppedicus") lies very near its adult position. This developmental transformation recapitulates one of the phylogenetic transformations suggested by comparison of adult Reptilia.

On the seventh day (stage IV), the cranial and caudal masses are fully differentiated from each other, having separate origins, insertions and fiber directions (Fig. 10). Different growth and differentiation patterns are also clearly evident. The cranial mass has grown very little in size since stage III but has differentiated rapidly, and Mm. iliotrochanterici cranialis and medius have separated. Their differentiation into two separate muscles is from an anlage originating throughout ontogeny entirely from the ilium. This division recapitulates another of the inferred phylogenetic transformations. The insertions of both muscle masses lie distal to the positions they attain in subsequent developmental stages. The proximal migrations of these insertions are also recapitulations of historic transformations. The M. iliofemoralis internus ("cuppedicus") is also completely separate at this stage and is overlapped proximally by the bellies of Mm. iliotrochanterici cranialis and medius. These three muscles originate entirely cranial to the acetabulum and have the same innervations and positions relative to each other that the divisions of M. PIFI maintain throughout life in Crocodylia (compare Figs. 3 and 10b). This similarity in positional criteria is only temporary, however, and later in avian ontogeny M. iliofemoralis internus ("cuppedicus") shifts to a position ventral to the other muscles.

The caudal mass has the opposite growth/differentiation pattern. It has grown rapidly in size since stage III, but is little differentiated. This mass will divide to become the adult Mm. iliofemoralis externus and iliotrochantericus caudalis (renamed below "iliofemoralis cranialis"), and this division recapitulates another of the inferred historic transformations. However, at stage IV both still have a common origin and insertion and are separated by only a slight cleft near their origin. The caudal mass inserts on the shaft of the femur well distal to the insertions of Mm. iliotrochanterici cranialis and medius, far from the insertions on the trochanter femoris attained by its adult derivatives.

By the eighth day (stage V), the insertion of the caudal mass has shifted proximad, passing laterad to the insertions of Mm. iliotrochanterici cranialis and medius, and inserts in a new position proximal to them on the trochanter femoris. This recapitulates another of the inferred historic transformations. At this time, Mm. iliofemoralis externus and iliotrochantericus caudalis "iliofemoralis cranialis" have clearly begun to differentiate but still have a common origin (Fig. 11).

Under the hypothesis of homology proposed here, five of the seven transformations inferred in avian history from comparison of adult Reptilia can be observed during development of the chick. The two recapitulations that do not occur are the shifts in position of origin onto the ilium of the homologs of the two divisions of M. PIFI. The absence of these recapitulations may result from accelerated growth of the ilium, relative to the growth rate of the deep dorsal myoblastic tissue. If this is true, the avian ilium may simply grow quickly forward over the ancestral lumbar region, covering the area where the divisions of M. PIFI historically arose, blocking passage of the myoblastic tissue into its ancestral region of differentiation.

In each of the five characters in which the transformations can be observed, it is possible to view Aves as possessing both the primitive archosaurian condition, which obtains only during early ontogeny, and the derived, uniquely avian state. The ontogeny of these characters thus exhibits a taxic (set within set) relationship that reflects the position of Aves as a group within the more inclusive taxon Archosauria. This is not an indication that crocodilians are ancestral to Aves, as some authors have recently argued (e.g., Martin et al., '80; Martin, '83a,b). Rather, it attests that all archosaurs pass through similar early developmental stages that, in Aves, may continue to change as ontogeny progresses.

It is evident that the three iliotrochantericus muscles do not possess a common history after the sixth day of ontogeny. The divergence of their separate pathways is one of the earliest events in the development of the deep thigh muscles, occurring before any of the individual iliotrochantericus muscles differentiates (Fig. 12). Consequently, grouping these muscles under a single name has only topographic significance. Previous authors have also attached phylogenetic significance to this grouping. In a phylogenetic context, however, "iliotrochantericus group" is a misnomer. The name itself appears to have been a principal source of confusion in understanding the homologies of these muscles, having led previous students to seek a single homolog for all three muscles. So that nomenclature can more accurately reflect the homology of these structures, a revision is discussed below.

Deep thigh muscles within Aves

Under previous views of deep dorsal thigh muscle homology, variations within and among avian species have been subject to conflicting interpretations. McGowan ('79), for example, reported that in one of two specimens of *Apteryx*, M. iliotrochantericus medius was present but M. iliotrochantericus cranialis, a muscle usually present in *Apteryx* and other ratites, was anomalously absent. Vanden Berge ('82) argued that

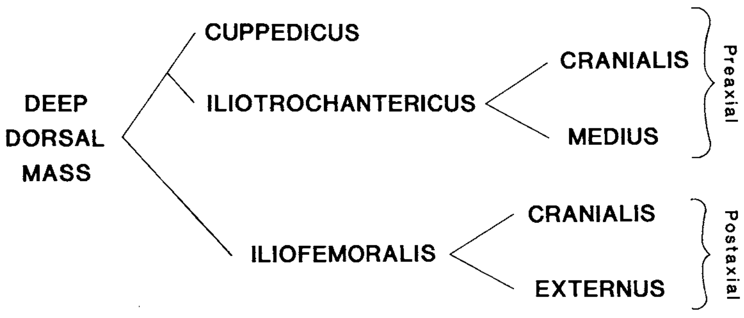

Fig. 12. Ontogeny of the deep dorsal thigh musculature of the chick.

McGowan's interpretation presented an unusual situation because, when only one of these two muscles is present, as is the case in many birds, it is generally M. iliotrochantericus cranialis, while M. iliotrochantericus medius is considered to be absent. Vanden Berge ('82), however, also correctly indicated that when only one of the two muscles is present, it is simply *a matter of convention* to call it iliotrochantericus "cranialis" rather than "medius," and that the homology of the single muscle has never been determined. Hudson ('37) employed this convention when he recommended addition to the phenetic "Garrod muscle formula" of variants of M. iliotrochantericus medius, but not M. iliotrochantericus cranialis, whose presence he considered to be constant. George and Berger ('66) also followed this convention in their choice of names. They argued, however, that situations where only one of these muscles is present are not a result of loss of the second muscle, but instead represent fusion of the two. They claimed that "...the fusion of these two muscles [Mm. iliotrochanterici cranialis plus medius] is an example of the tendency toward fusion of muscles which arise from contiguous areas and whose fibers are essentially parallel" (p. 392). Thus, when only one of the two muscles is present, previous authors have disagreed as to whether one muscle has been lost and if so, which, or whether the two have fused.

In contrast to these views, comparison of adult attributes in birds with other reptiles and the early development in the chick suggests that when only one muscle is present, it is because the common anlage of Mm. iliotrochanterici cranialis and medius fails to differentiate during ontogeny. The homolog of these muscles is undivided in Crocodylia, *Sphenodon*, and Chelonia; hence its differentiation into the two iliotrochantericus muscles is a condition that evolved within Archosauria, following the divergence of Aves and Crocodylia from their most recent common ancestor. Because Mm. iliotrochanterici cranialis and medius generally differentiate in Ratitae (Gadow, 1880; George and Berger, '66), as well as in most neognaths (George and Berger, '66), this condition appears to have been the ancestral state for Aves rather than arising during subsequent diversification within the group.

The M. iliotrochantericus is undifferentiated ("iliotrochantericus medius is absent") in *Sula, Fregata, Ardea, Butoroides, Sagittarius, Accipiter, Buteo, Aquila, Circus, Pandion, Falco, Polihierax, Fulica, Totanus, Uria, Tauraco, Otis, Bubo, Chordeiles, Chaetura,* and Cuculidae (George and Berger, '66, p. 392). Partial differentiation of the two has also been described. For example, George and Berger ('66, p. 392) reported that "in the Sandhill Crane, Mm. iliotrochantericus anterior et medius are separate at their origins only; the bellies fuse distally and insert by a common wide (1.5 cm) aponeurosis. In the right hip of one specimen, the two muscles were completely fused, so that the complex was represented by a single muscle mass, arising from the same area occupied by both muscles in the other dissections." Non-differentiation or partial differentiation of the two iliotrochantericus muscles in these neognaths is probably a result of neoteny (e.g., Gould, '77) evolving within Aves. One reason for uncertainty, however, is that the timing of its differentiation is known only in the chick. Until the timing of this event is known from a broader comparative sample, it remains possible that presence of the undifferentiated M.

iliotrochantericus simply reflects immaturity of this character in the specimen at hand. Avian specimens are usually considered "adult" if they have mature plumage. But because different anatomical systems develop at different rates, the presence of adult plumage may not necessarily indicate the cessation of muscular development in all species.

In light of the preceding argument, the current nomenclatural convention of referring to the undifferentiated M. iliotrochantericus as "iliotrochantericus cranialis" is seen incorrectly to imply differentiation of two muscles, followed by loss of one of them or fusion of the two. When only one muscle is present, it may be referred to simply as "iliotrochantericus." This nomenclature serves more accurately to distinguish the single muscle from its two derivatives, Mm. iliotrochantericus cranialis and iliotrochantericus medius, and reflects the hierarchies of muscle ontogeny and phylogeny. The M. iliotrochantericus caudalis, however, shares neither unique phylogenetic nor ontogenetic history with Mm. iliotrochanterici cranialis or medius, but it does share a unique common pathway with M. iliofemoralis externus during both ontogeny and phylogeny. Accordingly, I suggest that it be renamed "iliofemoralis cranialis" (see below), to reflect more accurately both its phylogeny and ontogenetic pathway, and to avoid confusion with M. iliotrochantericus and its two derivatives.

Variations in the derivatives of the caudal division of the deep dorsal mass are currently referred to using a similar convention. In most "non-passerine" birds, including Ratitae (Gadow, 1880) and Tinami (George and Berger, '66), the caudal mass divides to form Mm. iliofemoralis externus and iliofemoralis cranialis (="iliotrochantericus caudalis"). In adult passerines and a few "non-passerines," the caudal mass fails to divide and only a single muscle is present. When this is the case, the single muscle has been called "iliotrochantericus caudalis," and iliofemoralis externus is said to be absent. In light of the ontogenetic and phylogenetic histories described above, this convention is also misleading. The single, undifferentiated muscle can most accurately be called M. "iliofemoralis," and its derivatives, where present, can be distinguished as iliofemoralis externus and iliofemoralis cranialis, the latter name replacing "iliotrochantericus caudalis" (see below). George and Berger ('66) report the undifferentiated M. iliofemoralis ("iliofemoralis externus absent") in "*Spheniscus, Podiceps, Columba, Zenaidura, Goura, Gallicolumba, Didunculus,* Cuculidae, *Chordeiles, Apus, Eugenes, Pharomachrus, Chloroceryle, Momotus, Coracias, Eurystomus, Upupa, Aceros, Indicator, Colaptes, Dendrocopos, Procnias,* and all other passerines examined" (p. 393). This state is reported to be the general condition for Piciformes (Swierczewski and Raikow, '81) and Coraciiformes (Maurer and Raikow, '81).

From the distribution of M. iliofemoralis and its derivatives alone, one might conclude that Passeriformes, Piciformes, and Coraciiformes are primitive among birds, because they share the same condition (non-division of M. iliofemoralis) found in Crocodylia, Lepidosauria, and Chelonia, whereas in other birds M. iliofemoralis is divided. However, because they also possess many other characters that are derived within Aves (e.g., Raikow, '82), there is general agreement that passerines are highly derived among birds; it has never been suggested that passerines are the plesiomorphic sister group to all other living birds (e.g., Mayr and Amadon, '51; Wetmore, '60; Feduccia, '80; Cracraft, '81). Consequently, it is most parsimonious to view differentiation of Mm. iliofemoralis cranialis and externus as a derived condition for Aves generally, distinguishing Aves from other reptiles, and that the condition in passerine birds evolved from this state (Raikow, '82).

It thus appears likely that non-differentiation of M. iliofemoralis in Passeriformes, Piciformes, and Coraciiformes is a reversal, evidently the result of a neotenic truncation of the primitive avian ontogenetic pathway of these muscles (Raikow, '75; Raikow et al., '79; Hall, '84). This interpretation is further supported by the anomalous occurrence of M. iliofemoralis externus in one or a very few specimens of several passerines species. It was reported in the sturnids *Acridotheses tristis* (Raikow, '75) and *Leucopsar rothschildi* (Raikow, et al., '79), the bowerbird *Chlamydera nuchalis* (Ptilonorhynchidae), two species of *Epimachus* and *Loria loriae* (both Paradisaeidae), and the turnagrid *Turnagra capensis* (Raikow et al., '79). Its presence in these taxa suggests that the genetic information and developmental pathway leading to differentiation of Mm. iliofemoralis externus and cranialis is fully conserved in birds generally, and that phenotypic expression of this program is regulated heterochronically (Raikow, '75; Raikow et al., '79; Hall, '84).

Nomenclature

In a comprehensive review of avian myological nomenclature, Vanden Berge ('79, p. 175) concluded that the avian deep thigh musculature is second only to the muscles of the hand for nomenclatural confusion. The path toward a solution to this problem is clearly marked by general agreement on the goal of avian myological nomenclature. George and Berger ('66, p. 225) stated that "Ideally every avian anatomist would like to have a set of names which would indicate the homology of each muscle, not only among all birds but also in other vertebrate classes." Bock ('74, p. 136) agreed, stating that "The desired goal [of avian myological nomenclature] is to apply the same name to homologous anatomical features throughout birds, or tetrapods, or even vertebrates if that is possible." More recently, in the introduction to the *Nomina Anatomica Avium* [NAA], Baumel et al. (1979, p. ix) explained that "In all anatomical nomenclatures it seems to have been easier to defend the *status quo* than to attack it ... Nevertheless the *NAA* has eliminated some substantial errors in the prevailing usage, particularly those founded on inaccurate anatomical beliefs or incorrect homologies." As argued above, current nomenclature does not accurately reflect the homologies of the avian deep thigh muscles. Moreover, this has proved a source of misdirection at higher levels of study, leading previous students to seek a single homolog in other Reptilia for all three of the so-called iliotrochantericus muscles in Aves. This in turn resulted in acceptance of a more complex view of the evolution of the avian thigh than is warranted by available data. Revision of the nomenclature of these muscles thus appears necessary.

The nomenclature I recommend is presented in Figure 12 and Table 1. Following the arguments presented above, I suggest that the names "iliotrochantericus cranialis" and "iliotrochantericus medius" be retained in their current usage, but that "iliotrochantericus caudalis" be dropped. The Mm. iliotrochanterici cranialis and medius share unique historical and ontogenetic pathways, and this is accurately reflected in their current nomenclature. However, when only one muscle is present, it is most accurately referred to simply as "M. iliotrochantericus." The convention of referring to the undivided M. iliotrochantericus as "iliotrochantericus cranialis" is misleading and should therefore be abandoned in phylogenetic studies.

As discussed above, the muscle currently referred to as "iliotrochantericus caudalis" shares with M. iliofemoralis externus a unique pathway of development and descent. I suggest that our current understanding can more accurately be reflected by using the new name "iliofemoralis cranialis" to replace iliotrochantericus caudalis, while maintaining the term "iliofemoralis externus" in its current usage. If undivided, the single muscle should be called "M. iliofemoralis." In this way, the hierarchies of muscle ontogeny and phylogeny for the two iliotrochantericus muscles and the two iliofemoralis muscles are preserved in a hierarchical naming structure.

The last decision necessitates renaming M. iliofemoralis internus because its ontogeny and history are quite distinct from those of the other "iliofemoralis" muscles. To maintain its present name would imply a false identity, and this seems a greater evil than the inevitable disruption of changing its name. The disruption might be minimized if a previously used name could be resurrected, but I have been unable to find a suitable synonym. "Iliacus" (Hudson, '37; George and Berger, '66) and "psoas" (Howell, '38; Fisher, '46) were used in the past, but both names imply identity of the avian muscle with the uniquely mammalian muscles for which the names were coined. No evidence currently supports this implication and, if homology is to be the criterion for organizing nomenclature, both are therefore misnomers when applied to the avian muscle. As discussed above, "iliofemoralis internus" is homologous with the one division of M. PIFI medialis in Crocodylia, but using this name for the avian "iliofemoralis internus" would imply unique relationship with the avian M. pubo-ischio-femoralis (= M. adductor longus et brevus), which greatly differs developmentally and historically from the deep dorsal mass derivatives. There seems no choice but to coin a new name.

I take this course with reluctance, because it will be the fourth name to be applied to this single structure, and even this course poses difficulties. Traditionally, muscle names are based on their position of origin and insertion, or function. However, this practice predates by centuries the theory of evolution and a historic conception of homology (Russell, '16). When these attributes are transformed between homologous muscles, or when non-homologous muscles evolve similar attachments or functions, nomenclatural ambiguities such as the present one may result. It is not surprising to find need of revision of nomenclature for muscles so named, in order that their evolutionary histories may be more accurately depicted and studied. Christening the muscle, i.e., naming it as an individual, rather than its individual attributes (which may transform without affecting its individuality) seems the best solution. I suggest the name "*Cuppedicus*," from the Latin "cuppedia" (also cupedo-), meaning titbit or delicacy. This term alludes to the minute size and delicate structure of the muscle, but without direct reference to other formally named anatomical structures.

DISCUSSION

The ancestral state of the deep dorsal thigh musculature in Reptilia is reflected in those attributes still shared by adult turtles and lepidosaurs. There was an undivided, dually innervated M. iliofemoralis, and the M. PIFI was divided into two bellies that both originated from the dorsal surface of the puboischiadic plate. In some turtles both divisions of PIFI have expanded onto the shell, and in trionychids the iliofemoralis divides into two heads, both of which are states unique to turtles. The ancestral reptilian condition was inherited unchanged in Sauria and is largely preserved in the extant *Sphenodon*. Division of PIFI into three parts occurs in some Squamata, but since this state is known only in squamates, it cannot be construed as the ancestral state for Sauria, Lepidosauria, Archosauria, or Aves, as some authors have suggested.

In ancestral Archosauria, all primitive reptilian attributes were conserved, except that both divisions of M. PIFI had shifted their position of origin away from the puboischiadic plate. They probably originated beneath the sacral and lumbar portions of the vertebral column, with M. PIFI dorsalis overlapping broadly the belly of M. PIFI medialis laterally, as in extant crocodilians and early stages in ontogeny of the chick. In all birds, the ilium is expanded forward over the region where M. PIFI originates in crocodilians, and as a result its avian homologs (iliotrochanericus and cuppedicus) originate throughout ontogeny from the ilium. At no stage of ontogeny examined here are the positions or relations of these avian muscles similar to those of PIFI in adult turtles or lepidosaurs. However, early in avian ontogeny, Mm. iliotrochantericus and cuppedicus bear unique resemblance to the divisions of M. PIFI of adult crocodilians in their fiber directions, and positions relative to the vertebral column, lumbar plexus, and the other deep thigh muscles. Birds thus appear to conserve nearly all of the ancestral archosaurian character states, although in many species their expression is confined to early ontogeny, and later uniquely avian modifications obscure the resemblance in adults.

In Aves ancestrally, the embryonic deep dorsal mass differentiated into five adult muscles. The embryonic postaxial division of the deep dorsal mass differentiated to form Mm. iliofemoralis cranialis (= iliotrochantericus caudalis) and iliofemoralis externus, while the preaxial portion divided twice, forming Mm. iliotrochanterici cranialis and medius, and cuppedicus (= iliofemoralis internus). The presence of five adult derivatives of the deep dorsal mass is thus an apomorphy diagnostic of Aves. Another state derived for Aves is the relative size of the deep muscles. In all other reptiles, M. PIFI is a powerful muscle that is larger than M. iliofemoralis, but in birds iliofemoralis is greatly expanded and relatively much larger than the avian homologs of PIFI. Two additional avian apomorphies are that the homologs of PIFI take origin entirely from the ilium, and that all five deep dorsal derivatives insert on the proximal-most part of the femur, instead of on the femoral shaft, as in other Sauria. These ancestral avian states are conserved and expressed in fully mature ratites, tinamous, and many neognaths. The presence of fewer than five muscles in some neognaths and occasional ratite specimens probably represents a heterochronic perturbation of the fully conserved ancestral avian developmental program. It may also be possible in some instances that fewer than five adult muscles simply reflects immaturity of the specimen at hand.

Previous interpretations of deep thigh muscle homology promoted a view of the evolution of the avian hip in which its muscles had been subject to possible losses, reappearances, new appearances, fusions, changes in innervation, and changes in action. This view reflected an extremely plastic system, having passed through a multitude of evolutionary changes over its long history. However, it now appears more likely that the ancestral reptilian state of the deep thigh musculature is largely conserved in Archosauria. The ancestral archosaurian condition is in turn largely conserved in Aves, though obscured in adult birds by uniquely avian modifications. This interpretation suggests that few myological changes accompanied the shift from quadrupedality to bipedality, despite the associated profound modification of the skeleton.

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