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The Comparative Myology of the Thigh and Crus in the Salamanders *Ambystoma tigrinum* and *Dicamptodon tenebrosus*

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ABSTRACT Variation in myology of the hind limb among salamanders has been poorly characterized. Nineteen major hind limb muscles of *Ambystoma tigrinum* (Ambystomatidae) and *Dicamptodon tenebrosus* (Dicamptodontidae) were studied to provide baseline descriptive data on hind limb myology in salamanders and to generate hypotheses of hind limb muscle function. Most superficial muscles of the hind limbs span multiple joints, including a unique three-joint muscle, the ischioflexorius, that extends from the pelvic girdle to the plantar fascia. The deeper hind limb muscles span single joints. No myological differences were observed between the hind limbs of *A. tigrinum* larvae and individuals that had just metamorphosed. Fully adult tiger salamanders that had been housed in terraria for many years had hypertrophied femorofibularis and ischiofemoralis muscles, a condition similar to that reported in *Paramesotriton* and *Taricha,* which engage in terrestrial locomotion. In contrast, adults of *D. tenebrosus,* which are also good walkers, possess a hypertrophied ischioflexorius muscle and a reduced femorofibularis. These regular myological differences, and those described by previous workers for different salamander taxa, may be associated with differences in life-history traits, and in the case of *A. tigrinum,* with patterns of muscle use.

Although salamanders have long been used in kinematic studies seeking to elucidate the probable locomotor pattern of primitive tetrapods (Barclay, '46; Daan and Belterman, '68; Peters and Goslow, '83; Sukhanov, '74; Szekely et al., '69), relatively little is known about the extent of variation in hind limb musculature among salamander families. Aside from the thorough anatomical descriptions of Francis ('34) on *Salamandra salamandra* (Salamandridae) and Baird ('51) on *Pseudoeurycea bellii* (Plethodontidae), salamander hind limb myology is poorly described. It is as yet unclear to what extent the morphological patterns described for *S. salamandra* and *P. bellii* represent a general urodele pattern. Early workers (e.g., Emerson, '05; Mivart, 1869; Smith, '27) generally named urodele muscles after the mammalian or saurian muscles they most resembled in position and presumed function (though Mivart, 1869, was careful to disclaim any necessary implication of homology). Without clear knowledge of muscle homologies, different workers assigned muscles a host of different names (Francis, '34; Table 1), or assigned several different muscles to a single name. (Table 1; cf. Mivart's, 1869, and Smith's, '27, designations for the M. ischioflexorius and M. caudalipuboischiotibialis.)

Muscle homologies between urodeles and other tetrapod groups remain incompletely resolved. Appleton ('28) exhaustively reviewed the homologies of the post-axial thigh muscles in the different tetrapod groups, based on peripheral innervation patterns. Romer and Parson's ('77) homology chart remains the most up-to-date consideration of the problem, and they describe urodele limb musculature as "degenerate" (p. 273), and not reflective of the true primitive tetrapod condition. Given the obvious difficulty of unambiguously identifying equivalent muscles in salamanders and mammals (Roth, '88), urodele muscle names are now based largely on topological arguments. This approach not only circumvents the problem of identifying homologous muscles across major tetrapod taxa, but also is more informative of location within the limb than many mammalian limb

TABLE 1. Synonymy of salamander hindlimb muscles described for various genera[1]

Muscle	Francis ('34) *Salamandra*	Baird ('51) *Pseudoeurycea*	Emerson ('05) *Typhlomolge*	Gilbert ('73) *Necturus*	Mivart (1869) *Cryptobranchus*	Smith ('27) *Taricha*
Ischiocaudalis	Ischio-caudalis	Ischio-caudalis	Ischio-caudalis	Ischiocaudalis	*Ischio-caudal*	*Ischio-caudal*
Caudalipuboischiotibialis	Caudali-pubo-ischio-tibialis	Caudali-pubo-ischio-tibialis	Caudali-pubo-ischio-tibialis	Caudocruralis	Semimembranosus	Caudali-pubo-ischio-tibialis
Caudofemoralis	Caudali-femoralis	Caudali-femoralis	Piriformis	Caudofemoralis	Femoro-caudal	Femoro-caudal
Pubotibialis	Pubo-tibialis	Pubo-tibialis	Pubo-tibialis	Pubotibialis	—	Sartorius
Puboischiotibialis	Pubo-ischio-tibialis	Pubo-ischio-tibialis	Semitendinosus	Puboischiotibialis	Gracilis	Gracilis
Ischioflexorius	Ischio-flexorius	Ischio-flexorius	Semimembranosus	Ischioflexorius	Semitendinosus	Semimembranosus
Pubifemoralis	Pubi-femoralis	Pubi-femoralis	??	??	—	—
Puboischiofemoralis externus	Pubo-ischio-femoralis externus	Pubo-ischio-femoralis externus	Pectineus externus	Puboischiofemoralis	Adductor	Adductor
Puboischiofemoralis internus	Pubo-ischio-femoralis internus	Pubo-ischio-femoralis internus	Adductor	Puboischiofemoralis internus	Iliacus	Pectineus
Extensor iliotibialis, pars anterior	Extensor iliotibialis, pars anterior	Extensor iliotibialis, pars anterior	Ilio-extensor	Iliotibialis	Rectus femoris	Rectus femoris
Extensor iliotibialis, pars posterior	Extensor iliotibialis, pars posterior	Extensor iliotibialis, pars posterior	Ilio-extensor	Ilioextensorius	Glutaeus maximus	Glutaeus maximus
Iliofibularis	Ilio-fibularis	Iliofibularis	Ilio-fibularis	Iliofibularis	Ilio-peroneal	Ilio-peroneal
Iliofemoralis	Ilio-femoralis	Ilio-femoralis	Ilio-femoralis	—	Glutaeus medius/ minimus	Glutaeus medius/ minimus
Ischiofemoralis	Ischio-femoralis	Ischio-femoralis	Quadratus femoris	??	??	??
Femorofibularis	Femoro-fibularis	??	??	??	Biceps	Biceps femoris
Flexor primordialis communis	Flexor primordialis communis	??	??	Flexor primordialis communis	Flexor digitorum	Flexor communis digitorum
Extensor cruris tibialis	Extensor cruris tibialis	??	??	Extensor tibialis	Tibialis anticus	Tibialis anticus
Extensor digitorum communis	Extensor digitorum communis	??	??	Extensor digitorum communis	Extensor longus digitorum	Extensor longus digitorum
Extensor cruris et tarsi fibularis	Extensor cruris et tarsi fibularis	??	??	Extensor fibularis	Peroneus	Peroneus

[1]The names in the first column are those used in the present study. –indicates muscle is missing. ?? indicates muscle is not described by the author.

muscle names. The terminology of Francis ('34) has largely been accepted by current workers, with a few notable exceptions in laboratory guides and textbooks (e.g., Gilbert, '73; Hildebrand, '74; Romer and Parsons, '77). In addition to strict anatomical description, Francis ('34) included a statement of the presumed functions of hind limb muscles with their anatomical descriptions, but these hypotheses have not been tested empirically. No attempt to correlate variation in hind limb muscle form among different salamander groups with locomotor function and life-history traits has been made. Basic morphological data such as that described herein are essential for the investigation and accurate interpretation of limb function, and, along with data on innervation and developmental patterns, for the future establishment of reliable muscle homologies.

Therefore, the goals of the present study are to (1) describe the myology of the thigh and crus in two species of salamander with robust limbs, the tiger salamander, *Ambystoma tigrinum,* and the Pacific giant salamander, *Dicamptodon tenebrosus;* (2) synonymize the muscles described herein with those described by earlier workers; and (3) discuss the variation found between and among the salamander species in relation to life–history traits.

MATERIALS AND METHODS

Fourteen specimens were dissected for this study. Three were larval *A. tigrinum* (University of Kansas Museum of Natural History, specimen numbers KU 89119, 89140–41), three recently metamorphosed *A. tigrinum* (i.e., within several months of gill resorption; KU 89102, 89107, 89108; all KU specimens collected from ponds near Colorado Springs, Colorado), two eastern morph adult tiger salamanders kept in the lab in small terraria for more than eight years, and six adult *D. tenebrosus* (Good, '89; Los Angeles County Museum of Natural History, specimen numbers LACM 73, 29417, 84541, collected in Humboldt County, California, University of California, Berkeley, Museum of Vertebrate Zoology, specimen numbers MVZ 18973, 44365, 44367). In addition, specimens cleared-and-stained for bone and cartilage were observed for skeletal details (*A. tigrinum:* personal collection; *D. tenebrosus:* California Academy of Sciences, specimen number CAS 18097).

All dissections and observations were performed with the aid of a Zeiss IVB microscope equipped with a camera lucida. The iodine stain described by Bock and Shear ('72) was used during dissections to aid in distinguishing connective tissue and muscle-fiber direction.

RESULTS

Nineteen major muscles of the thigh and crus are detailed below and are synonymized with the names given them by previous workers in Table 1. Though they are occasionally labelled in the figures, descriptions of the small, deep muscles of the crus and the intrinsic muscles of the foot are beyond the scope of this work, and the reader is referred to Francis ('34) and Schaeffer ('41). Muscle terminology follows that of Francis ('34), except where noted. The major skeletal features of the hind limb are shown in Figure 1. In general, the skin and connective tissue in the hind limbs of *Dicamptodon* are thicker and more dense than the corresponding structures in *Ambystoma.*

The muscles are described below in the following order: (1) muscles connecting the tail with the pelvic girdle and/or thigh, (2) ventral muscles arising from the pelvic girdle, (3) dorsal muscles arising from the pelvic girdle, (4) ventral muscles arising from the femur, and (5) dorsal muscles arising from the femur. Multiple muscles in the above groupings are described according to their position: anterior to posterior, and superficial to deep. In each case below, the muscle is described for larval *A. tigrinum,* followed by a description of variation seen in adult *A. tigrinum* and adult *D. tenebrosus.* In no case was any difference in form observed between the muscles of larval and just-metamorphosed *A. tigrinum.*

Caudal-pelvic girdle/femur muscles

M. ischiocaudalis (ISC)

The ischiocaudalis is the most superficial of the three straplike muscles running between the tail and the pelvic girdle/hind limb (Fig. 2A). It originates from the ventral myoseptum at the level of the third caudal (postsacral) vertebra. It is a parallel-fibered muscle, inserted via a long, flat, thin tendon onto the dorsal surface of the pubo-ischiac plate, posterior to the origin of the iliofemoralis (ILFM) and medial to the origin of ischiofemoralis (ISFM; Fig. 6A). The insertion tendon of the ISC covers the ventral surface of the most distal section of the muscle, and the superficial fibers turn ventrad to insert on it.

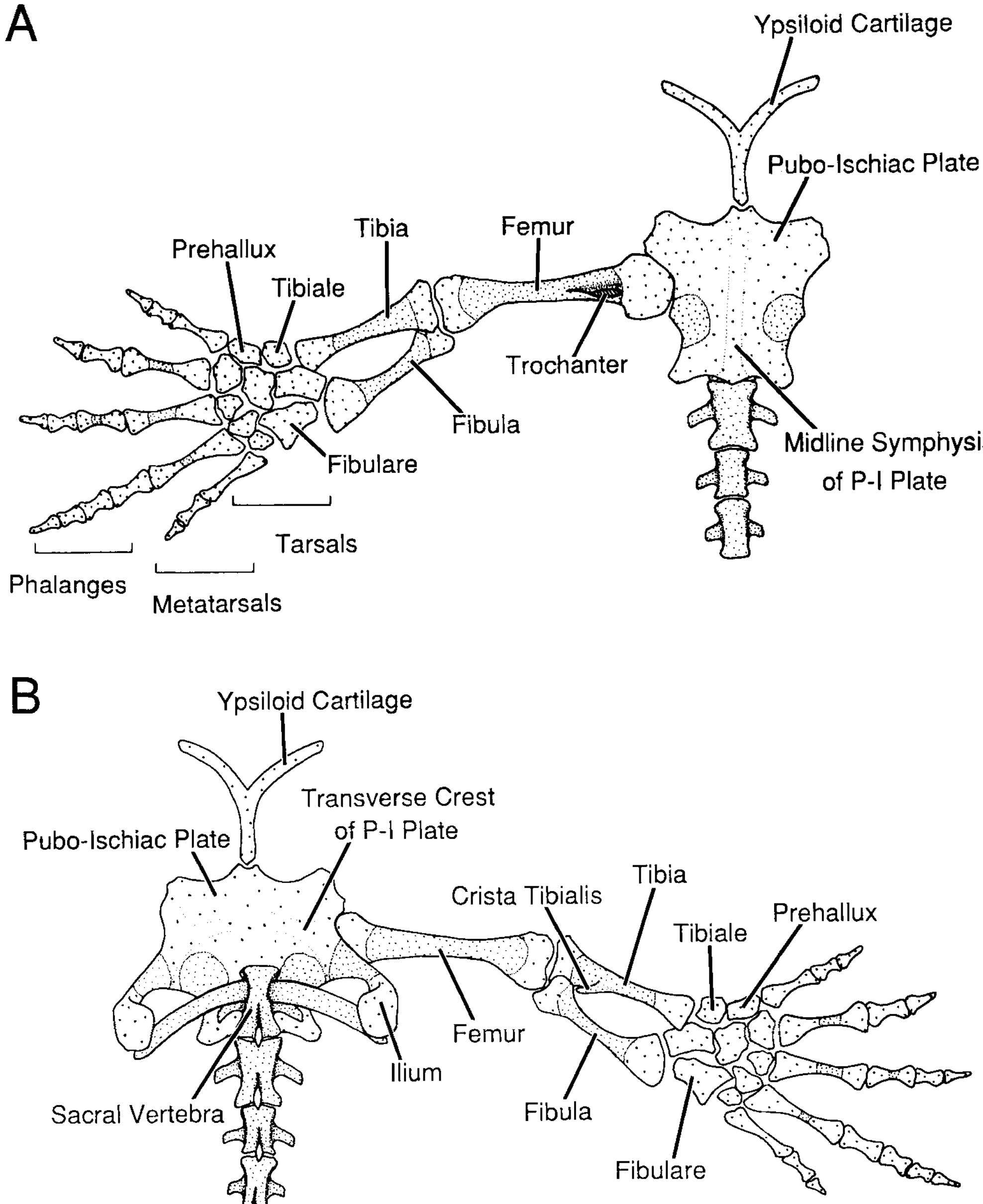

Fig. 1. *Ambystoma tigrinum.* Hind limb skeleton of right leg of transformed specimen, indicating major skeletal features. **A:** Ventral view. **B:** Dorsal view. In this and succeeding figures, coarse stippling indicates cartilage; fine stippling indicates bone. Anterior is toward the top of the page.

Variation: In *D. tenebrosus,* this straplike muscle has a stout tendon of insertion, and the muscle as a whole twists about its long axis in a ventromedial direction as it passes from origin to insertion (Fig. 2B).

M. caudalipuboischiotibialis (CPIT)

This straplike muscle lies immediately dorsal to the ISC. It arises via a short, thin aponeurosis from the third postsacral verte-

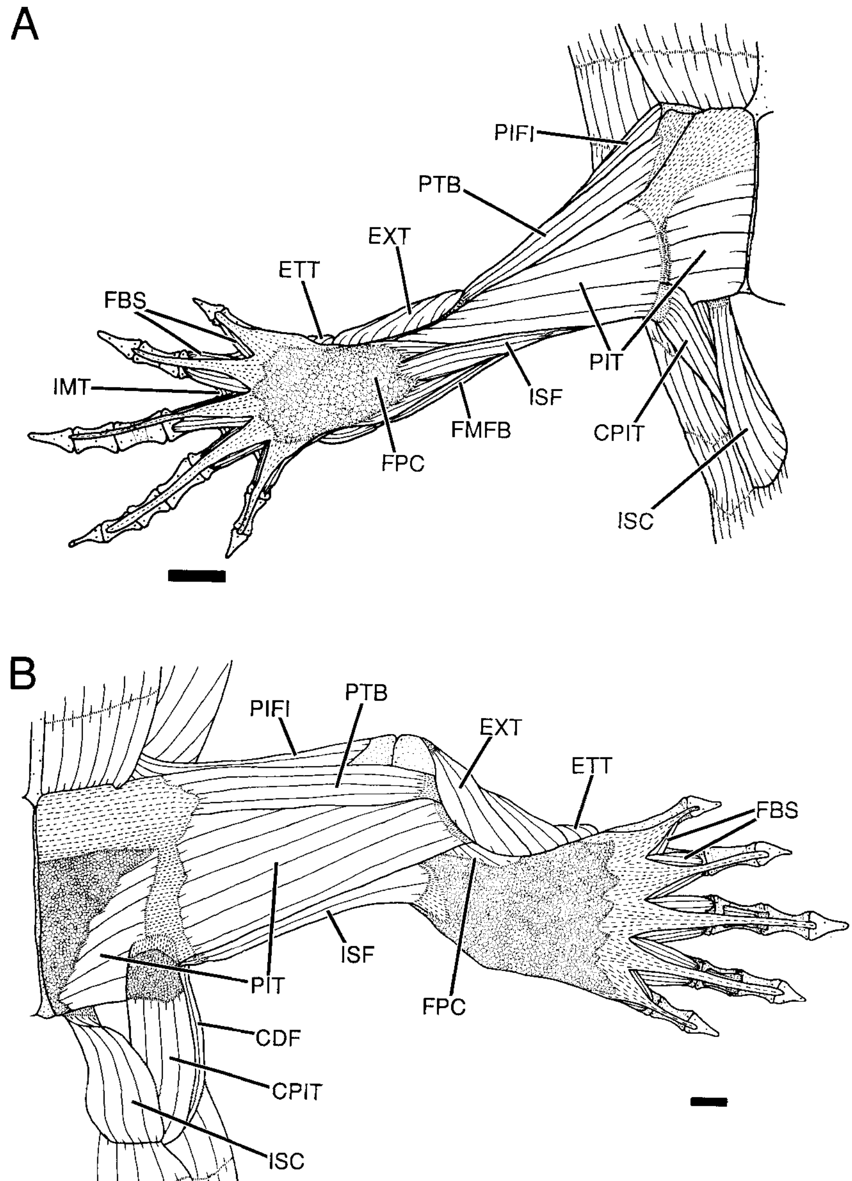

Fig. 2. Superficial ventral hind limb musculature. **A:** *A. tigrinum*, KU 89141. Right leg. **B:** *Dicamptodon tenebrosus*, MVZ 18973. Left leg. In this and the following figures, attachment points of the muscle are indicated by the hash marks at the ends of the fibers. Tendons are designated by dashed lines, and surface aponeuroses to which muscle fibers attach are indicated by the hexagonal stippling pattern (e.g., the insertion of FPC on the plantar fascia). Abbreviations for this and succeeding figures are as follows: CDF, M. caudofemoralis; CPIT, M. caudalipuboischiotibialis; EDB, Mm. extensores digitorum breves; EDC, M. extensor digitorum communis; ETT, M. extensor tarsi tibialis; EXF, M. extensor cruris et tarsi fibularis; EXT, M. extensor cruris tibialis; FBS, Mm. flexores breves superficiales; FMFB, M. femorofibularis; FPC, M. flexor primordialis communis; ILFB, M. iliofibularis; ILFM, M. iliofemoralis; ILTA, M. extensor iliotibialis, pars anterior; ILTP, M. extensor iliotibialis, pars posterior; IMT, Mm. intermetatarsales; IOC, M. interosseus cruris; ISC, M. ischiocaudalis; ISF, M. ischioflexorius; ISFM, M. ischiofemoralis; PFM, M. pubifemoralis; PIFE, M. puboischiofemoralis externus; PIFI, M. puboischiofemoralis internus; PIT, M. puboischiotibialis; PTB, M. pubotibialis. Scale bars = 2 mm.

bra (Figs. 1, 2A). It courses, parallel-fibered, anteriorly to insert by a thin, short aponeurosis onto the tendon dividing the proximal and distal portions of the puboischiotibialis (PIT). Like the ISC, the tendon of insertion covers approximately the distal tenth of the CPIT, and the superficial fibers of the muscle turn ventrally to insert on this aponeurosis.

Variation: In *D. tenebrosus,* the fibers of the CPIT originate directly from the third and fourth postsacral vertebrae and from the associated myosepta. It is unipinnate in arrangement; all fibers insert on an aponeurosis covering the surface of the distal one-tenth of the muscle. This connective tissue sheet in turn inserts onto the entire posterior surface of the tendon separating the proximal and distal halves of the PIT (Fig. 2B).

M. caudofemoralis (CDF)

This is the deepest of the three straplike muscles connecting the tail with the pelvic girdle and hind limb. The caudofemoralis (Gilbert, '73) arises via a short, flat aponeurosis from the third caudal vertebra (Fig. 1). It is parallel-fibered, and inserts via a strong, flat tendon onto the posteroventral border of the femur, just posterior to the femoral trochanter, approximately one-third of the way to the knee, between the insertions of the puboischiofemoralis externus (PIFE) and ILFM (Figs. 3A, 4A, 5A). The tendon of insertion is longer, and the muscle fibers correspondingly shorter, on the medial side of the muscle.

Variation: The CDF is thick in *Dicamptodon* (Figs. 3B, 4B, 5B) and easily separable into two or more distinct clumps of fibers. It arises from the third and fourth postsacral vertebrae and the associated myosepta, and inserts via a tough tendon onto a prominent knob of bone on the posterior face of the femoral trochanter.

Ventral pelvic girdle muscles

M. pubotibialis (PTB)

The pubotibialis is the most anterior superficial ventral thigh muscle. It is a narrow, parallel-fibered muscle that originates partially from the anterolateral border of the pubo-ischiac plate (Fig. 1) via a flat tendon, and partially from the superficial aponeurosis covering the anterior section of the PIFE. The deep fibers insert onto the proximal tibia, whereas the superficial fibers insert on a flat tendon that narrows as it courses distad to cover part of the insertion of the PIT; this tendon attaches to the bone along a line parallel to the insertion of the PIT (Fig. 2A). This muscle is difficult to separate cleanly from the PIT; bundles of fibers originating in one muscle may cross over to insert with fibers from the other. In one specimen (KU 89119), several fascicles originating with the PTB crossed to insert as part of the PIT.

Variation: In one *D. tenebrosus* specimen (LACM 84541), part of the muscle arose directly from the anterolateral corner of the pubo-ischiac plate, whereas other specimens had a purely tendinous origin such as described above. In all specimens, insertion was solely by a strong, flat, triangular tendon onto the proximal anteromedial surface of the tibia (Fig. 2B). The PTB is bound to the PIT by thick connective tissue, making the two muscles difficult to separate.

M. puboischiotibialis (PIT)

This large, parallel-fibered muscle originates directly from the posterior two-thirds of the ventral midline symphysis of the pubo-ischiac plate (Fig. 1). It is divided into distinct proximal and distal portions by a short tendon laterally at the level of the acetabulum (Fig. 2A). The fibers composing the posterior section of the proximal portion of the muscle insert on this tendon, whereas the anteriormost fibers insert onto a superficial aponeurosis covering the anterior section of the PIFE. The posterior fibers of the distal portion of the PIT originate from the intramuscular tendon, whereas the anterior fibers arise from the aforementioned aponeurosis. The fibers of the distal portion converge slightly to insert on the proximal two-thirds of the anteromedial face of the tibia. Most of the fibers insert directly onto the bone, but some of the most superficial fibers insert onto a small, triangular tendon that covers the anterior two-thirds of the insertion.

Variation: In *Dicamptodon,* the PIT assumes a more unipinnate fiber arrangement at its origin; deep fibers of the proximal section of the muscle originate directly from the posterior two-thirds of the midline symphysis of the pubo-ischiac plate, whereas the superficial fibers arise from a tough aponeurosis covering the proximal one-third to one-half of the proximal section (Fig. 2B). The fibers of the PIT insert on approximately the middle three-quarters of the medial surface of the tibia. All of the superficial fibers insert via a short, tough tendon, whereas the deep fibers insert onto the bone. In one specimen (LACM 84541), the most posterior fibers,

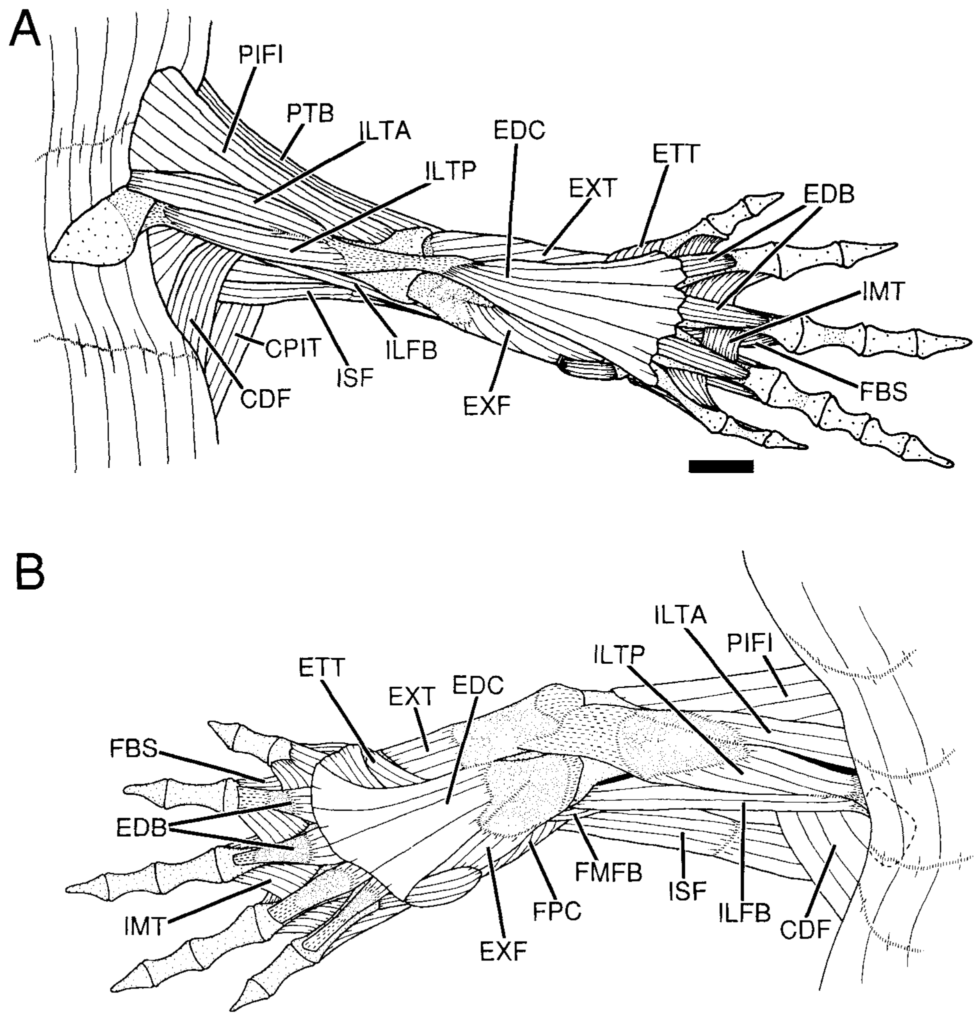

Fig. 3. Superficial dorsal hind limb musculature. **A:** *A. tigrinum,* KU 89141. Right leg. **B:** *D. tenebrosus;* MVZ 18973. Left leg. The dashed line indicates the shape of the ilium, which is hidden by thick epaxial musculature. Scale bars = 2 mm.

both superficial and deep, had a tendinous insertion. This specimen and one other (LACM 73) also had some fibers arising from the intramuscular tendon of ISF inserting with the fibers of PIT, and vice versa.

M. ischioflexorius (ISF)

This muscle is unique in that it crosses three joints. It originates by a short and stout (but relatively weak) tendon from the posterolateral corner of the pubo-ischiac plate (Fig. 1). It inserts onto the plantar aponeurosis via a short, flat tendinous sheet just above the level of the ankle. Like the PIT, the ischioflexorius is composed of proximal and distal portions, the two being divided by a tendinous plate at a level approximately one-third to one-half the distance between the origin and insertion of the muscle (Figs. 2A, 3A, 4A, 6A). Both portions are parallel-fibered, but the fibers of the distal section spiral from origin to insertion in a clockwise direction (Figs. 4A, 6A). The proximal portion is somewhat stouter than the distal portion.

Variation: In *D. tenebrosus,* the fibers of the ISF originate directly from the posterolat-

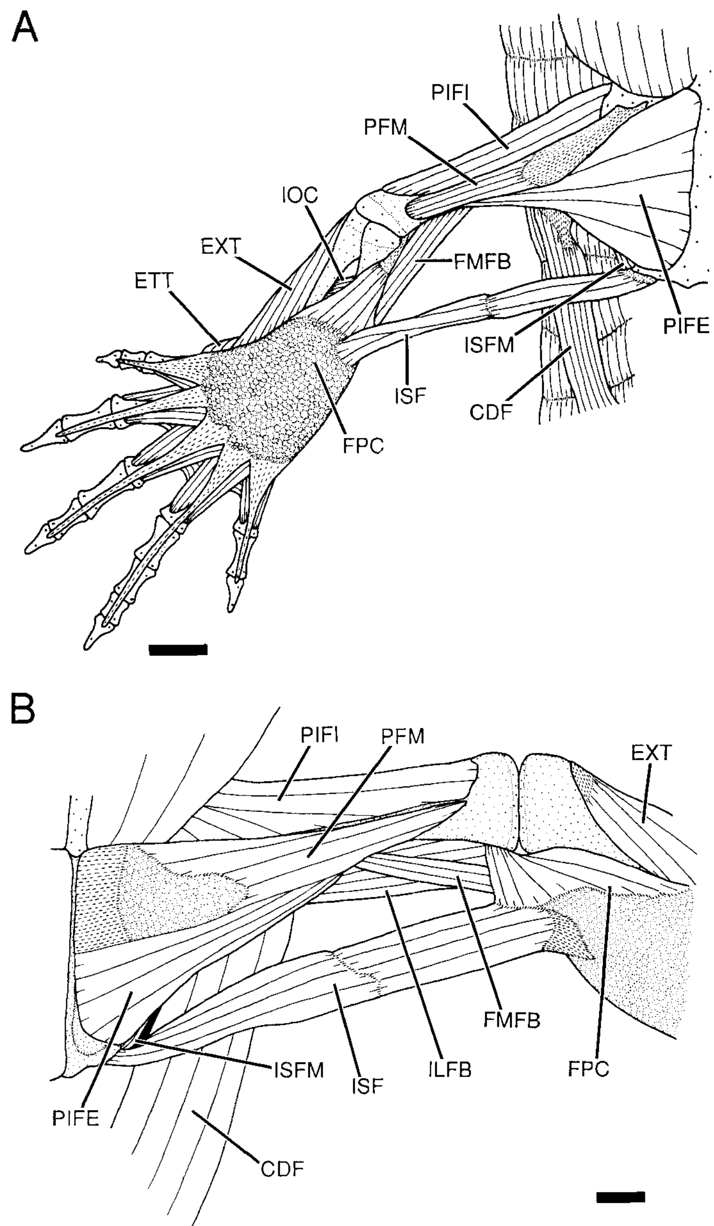

Fig. 4. Ventral hind limb musculature: CPIT, ISC, PIT, PTB removed. **A:** *A. tigrinum,* KU 89140. Right leg. **B:** *D. tenebrosus* (MVZ 18973). Left leg, distal crus and foot not shown. Scale bars = 2 mm.

eral corner of the pubo-ischiac plate (Figs. 2B, 3B, 4B, 6B). It has a broad insertion onto the surface of the plantar aponeurosis covering FPC, at a more proximal level than the insertion of this muscle in *A. tigrinum* (cf. Fig. 4A,B).

M. pubifemoralis (PFM)

The PFM is the most anterior of the ventral deep pelvic muscles (Fig. 4). The pubifemoralis arises, partially, from the ventral side of the anterolateral border of the pubo-

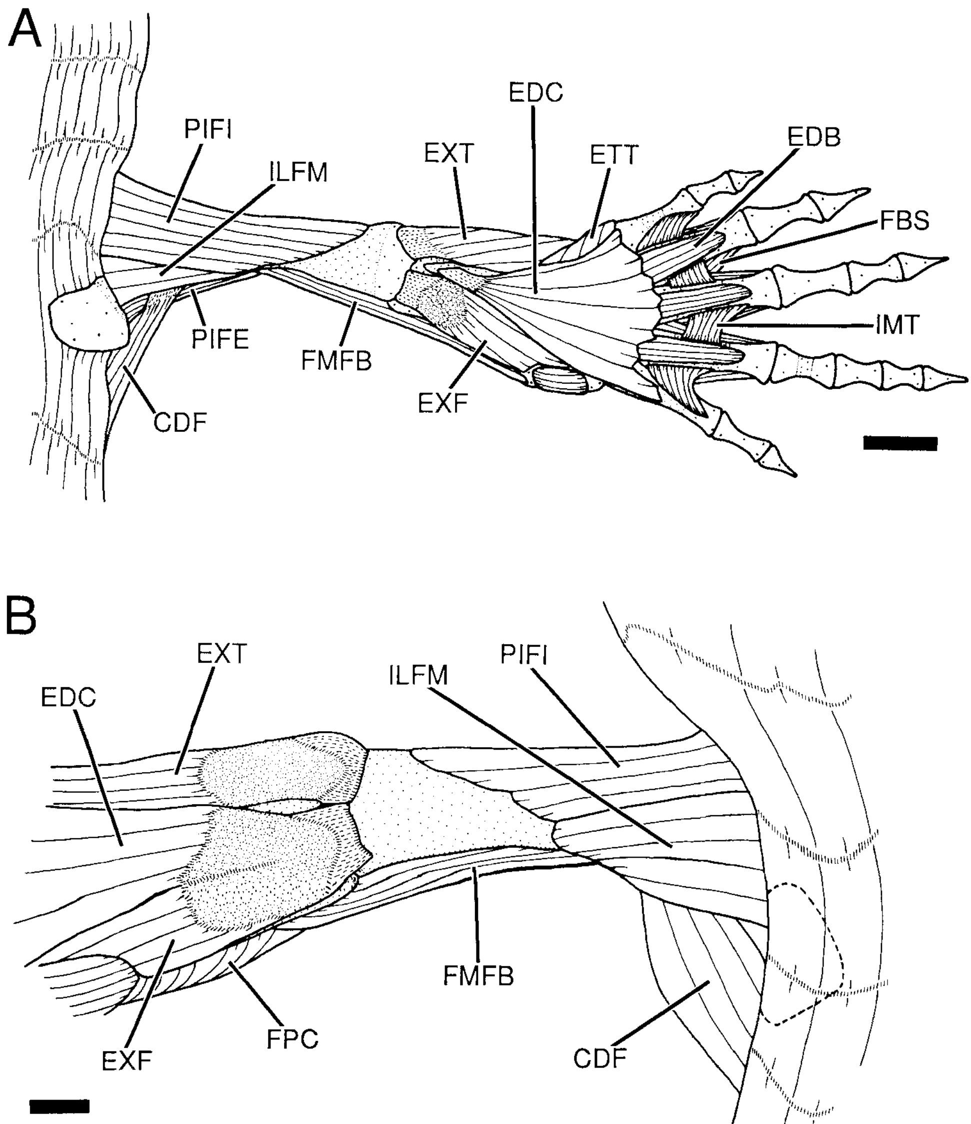

Fig. 5. Dorsal hind limb musculature: ILFB, ILTA, ILTP, ISF removed. **A:** *A. tigrinum*, KU 89140. Right leg. **B:** *D. tenebrosus* (MVZ 18973). Left leg; distal crus and foot not shown. The dashed line indicates the shape of the ilium, which is hidden by thick epaxial musculature. Scale bars for both panels = 2 mm.

ischiac plate (Fig. 1), and, partially, from the superficial aponeurosis covering the anterior portion of PIFE. It is a parallel-fibered muscle that crosses the hip joint to insert directly on the ventral border of the distal half of the femur (distal to the femoral trochanter; Fig. 4A). This muscle bears the same spatial relationship to the PIFE that the PTB does to the PIT (i.e., the PFM has a (partially) tendinous origin anterior to PIFE, overlies the anterior border of the PIFE, and inserts slightly anterior and proximal to, but immediately adjacent to, that of PIFE).

Variation: In *Dicamptodon,* the origin of the PFM (Fig. 4B) is entirely from the lateral portion of the aponeurosis covering the surface of the anterior one-third of the PIFE (though in LACM 73, the most anterior fibers arose directly from the ventral surface of the anterolateral border of the pubo-

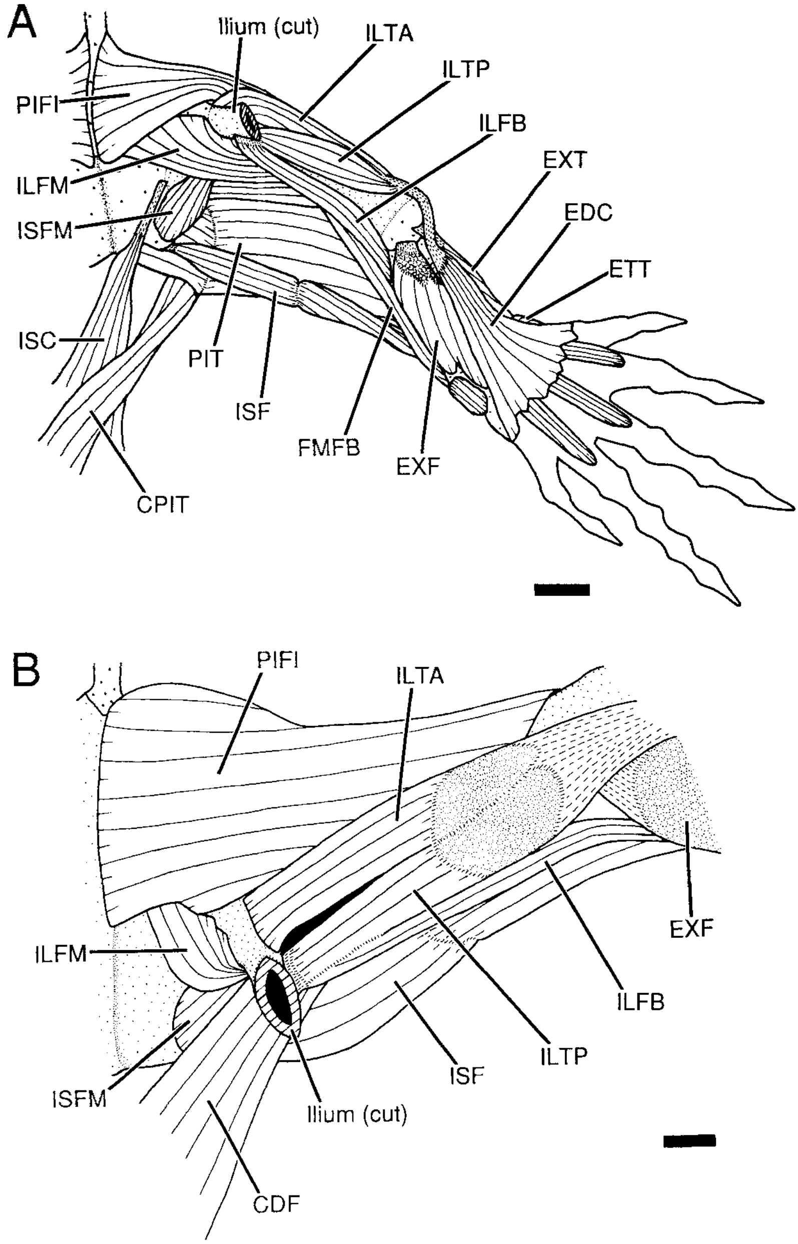

Fig. 6. Dorsal superficial hind limb musculature, with the ilium cut and deflected outward to expose the dorsal side of the pubo-ischiac plate. Right leg. **A:** *A. tigrinum* (KU 89141), CDF removed. Details of foot musculature not shown. **B:** *D. tenebrosus* (LACM 84541); CPIT and ISC removed. Distal crus and foot not shown. Scale bars = 2 mm.

ischiac plate). In one specimen of adult *A. tigrinum* (personal collection, 17), the origin was entirely from the aponeurosis covering anterior PIFE, at approximately the level of the lateral border of the pubo-ischiac plate.

M. puboischiofemoralis externus (PIFE)

The fibers of the puboischiofemoralis externus (Fig. 4A) originate directly from the entire length of the ventral midline symphysis and the medial two-thirds of the anterior border of the pubo-ischiac plate, and from the ventral surface of the pubis and ischium (Fig. 1). It is a fan-shaped muscle (though not pinnate in its fiber arrangement) whose fibers converge to insert directly onto both the anterior and posterior sides of the femoral crest and onto the ventral border of the femur distal to the femoral crest to a point approximately half-way to the knee, and via a short, strong tendon onto the femoral trochanter. No fibers of the PIFE originate from the connective tissue sheet covering its anterior portion.

Variation: In *D. tenebrosus,* the PIFE originates directly from the entire anterior border of the pubo-ischiac plate, the anterior two-thirds of the ventral midline symphysis, the medial ventral surface of the pubo-ischiac plate, and partially from the aponeurosis covering the anterior one-third of the muscle surface (partial unipinnate origin; Fig. 4B, 7C). All fibers insert onto the femoral trochanter; there is no tendinous insertion.

Dorsal pelvic girdle muscles

M. puboischiofemoralis internus (PIFI)

The puboischiofemoralis internus arises from the anterior two-thirds of the dorsal midline symphysis of the pubo-ischiac plate (Fig. 1), from the associated connective tissue separating the right and left PIFI's, from the lateral border of the posterior section of the ypsiloid cartilage, and (a few fibers) from the dorsal face of the pubis. It is a parallel-fibered muscle that curves around the anterior border of the ilium to insert directly onto the anterior face of the femur (Figs. 5A, 6A, 7A). The insertion extends ventrally to the base of the femoral trochanter and dorsally to abut the insertion of the ILFM.

Variation: The PIFI in *Dicamptodon* has a greater proportion of its fibers originating from the dorsal face of the pubis, and its insertion covers a greater area on the anterior face of the femur (Figs. 5B, 6B, 7B,C).

M. extensor iliotibialis, pars anterior (ILTA)

This spindle-shaped muscle arises directly from the anterolateral border of the ilium, just dorsal to the acetabulum (Fig. 1), between the ILFM and the passage of the PIFI around the anterior border of the ilium (Figs. 3A, 6A). It runs, parallel-fibered, along the dorsal face of the femur to insert in common with the ILTP on a wide, stout tendon that crosses the knee to insert on the crista tibia-

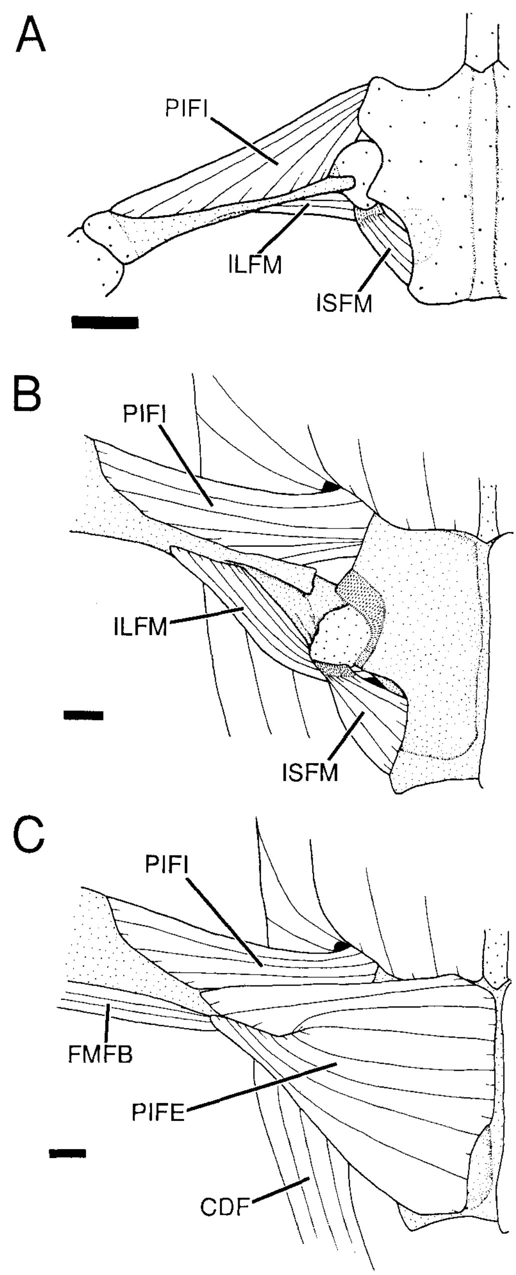

Fig. 7. Deep ventral pelvic musculature. Right leg. **A:** *A. tigrinum,* KU 89140. **B:** *D. tenebrosus,* LACM 84541. In A and B, all muscles except ILFM, ISFM, and PIFI have been removed. Note the difference in ossification of the pelvic girdle. **C:** *D. tenebrosus,* LACM 84541. ISF, PFM, PIT, PTB, and the aponeurosis covering the anterior section of PIFE have been removed to show the orientation of PIFE fibers. Scale bars in all panels = 2 mm.

lis (tibial spine). In some specimens this tendon also joined the connective tissue covering the proximal portions of the EDC and the EXT. The distal one-third of the ILTA is divided from the corresponding section of the ILTP by a tendinous plate; some of the posterior fibers of the ILTA insert on this tendinous sheet.

Variation: In one specimen of *D. tenebrosus* (LACM 84541), the most anterior fibers originate via a tough, flat tendon from the anterior border of the base of the ilium, above and medial to the acetabulum. In all specimens, the fibers are unipinnate in arrangement and insert onto an aponeurosis covering the distal one-quarter to one-half of the muscle, which continues as the common tendon of insertion with ILTP (Figs. 3B, 6B).

M. extensor iliotibialis, pars posterior (ILTP)

The extensor iliotibialis, pars posterior is a parallel-fibered muscle arising from the ilium via a fan-shaped tendon that runs dorsoventrally along the posterolateral border of the ilium dorsal to the acetabulum (Figs. 1, 3A, 6A). It is separated from the ILTA by a tendinous plate along the distal one-third of its length; some of the anterior fibers of the muscle insert on this tendon. The muscle as a whole inserts onto a common tendon with the ILTA. This tendon crosses the knee joint to insert on the tibial spine and (occasionally) on the connective tissue covering the proximal parts of the extensor digitorum communis (EDC) and the extensor cruris tibialis (EXT).

Variation: In *D. tenebrosus,* the fibers of ILTP insert onto a tough aponeurosis covering approximately the distal one-quarter of the muscle (unipinnate arrangement; Figs. 3B, 6B), which continues as the common tendon of insertion with ILTA.

M. iliofibularis (ILFB)

The iliofibularis originates from the posterolateral face of the tendon of origin of the ILTP (Figs. 3A, 6A). It is a parallel-fibered muscle that extends along the posterior face of the femur and crosses the knee joint to make a wedge-shaped insertion directly onto the posterior border of the fibula, proximal to and between the insertions of the femorofibularis (FMFB) and the extensor cruris et tarsi fibularis (EXF).

Variation: In *D. tenebrosus,* the ILFB is robust. It originates partially from the posterior surface of a common tendon of origin with ILTP, and partially from an aponeurosis covering the proximal one-tenth of the posterior surface of ILTP (Figs. 3B, 6B). It inserts via a short, flat tendon in the same position as described above for *A. tigrinum.*

M. iliofemoralis (ILFM)

The iliofemoralis is a parallel-fibered muscle originating directly from the lateral face of the ilium (just dorsal to the acetabulum), from the dorsal surface of the ischium (posterior to the transverse crest of the pubo-ischiac plate; Figs. 1, 5, 6, 8), and from the lateral border of the pubo-ischiac plate to a point approximately two-thirds of the distance to the midline symphysis. It inserts on the posterior surface of the femur, posterior to the insertion of the PIFI, and extends ventrally to the base of the femoral trochanter (Fig. 7). Those fibers that arise from the ilium consistently insert in a more dorsal position on the femur (just posterior to the insertion of the PIFI) than those arising from the ischium.

Variation: In both adult *A. tigrinum* and *D. tenebrosus,* the transverse crest of the pubo-ischiac plate is much more pronounced than in larval tiger salamanders and has a distinct hollow on its posterior side, from which many fibers of the ILFM originate.

M. ischiofemoralis (ISFM)

The ischiofemoralis is a stout, parallel-fibered muscle arising directly from the lateral border of the posterior one-third, and the lateral one-third of the dorsal surface of the pubo-ischiac plate (Figs. 1, 6, 7, 8, 9A). Its fibers arise in common with those of the posterior PIFE. The ISFM inserts via a strong, stout tendon onto a tuberosity on the posterior side of the head of the femur.

Variation: In four of the six *D. tenebrosus* specimens examined, the ISFM showed a (partial) bipinnate arrangement; on the dorsal side of the muscle, a tendon runs parallel to the long axis of the muscle in the distal one-quarter of the muscle (Fig. 9C). Superficial muscle fibers insert onto both sides of this tendon. The insertion of the ISFM is onto a strong tendinous capsule surrounding the femoral tuberosity described above. In adult *A. tigrinum,* the tendons of insertion of the ISFM and the PIFE seem to have grown together; they cannot be separated, and there is a continuous band of connective tissue extending from the tuberosity on the poste-

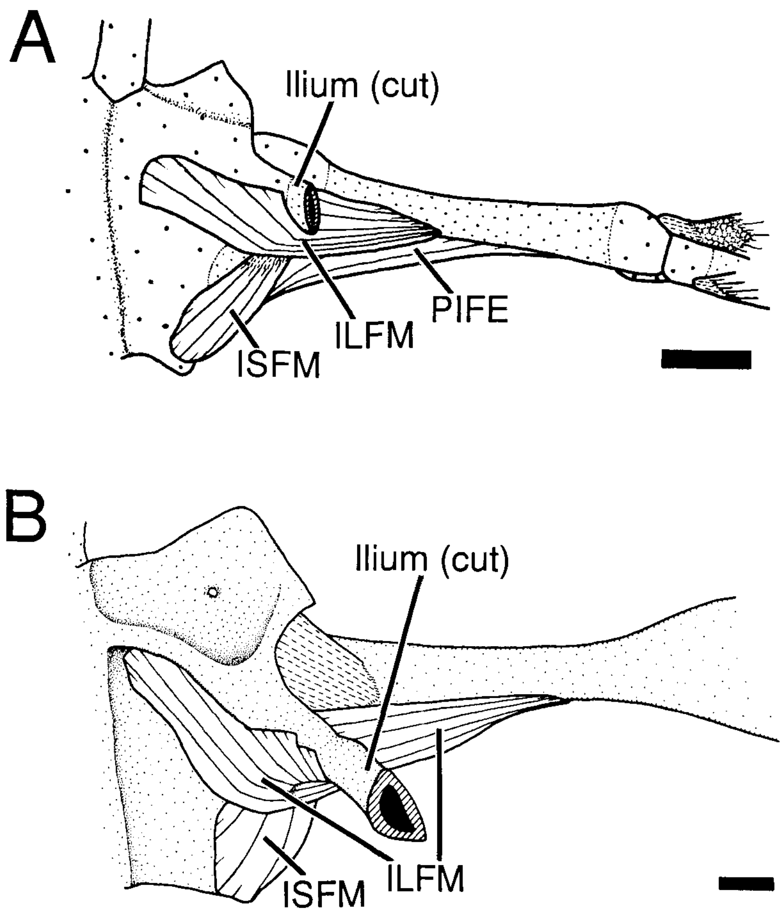

Fig. 8. Deep dorsal pelvic musculature. The ilium has been cut and deflected outward to expose the dorsal surface of the pubo-ischiac plate. ILFB, ILTA, ILTP, and PIFI have been removed. Right leg. **A:** *A. tigrinum,* KU 89141. **B:** *D. tenebrosus,* LACM 84541. Scale bars = 2 mm.

rior head of the femur to the posterior proximal surface of the femoral trochanter, with muscle fibers inserting along this entire expanse (Fig. 9B).

Ventral femoral muscles

M. femorofibularis (FMFB)

The femorofibularis arises directly from the posteroventral border of the femur, at a point approximately half-way to the knee (Fig. 1). It is a parallel-fibered muscle that crosses the knee joint to fan out and insert onto the posterolateral border of the fibula, between the insertion of the EXF and the fibular portion of the origin of the flexor primordialis communis (FPC; Figs. 4A, 5A, 6A). In two larval *A. tigrinum,* the fibers that inserted most distally on the fibula joined a short tendon on which a few fibers from the EXF inserted, and (in one larva) from which a few fibers of the FPC originated.

Variation: In *D. tenebrosus,* FMFB is a thin slip of muscle that originates via a short, thin tendon and inserts by way of another thin tendon on the posterolateral fibula approximately one-quarter of the way from its proximal end immediately posterior to the insertion of EXF (Figs. 4B, 5B). The FMFB is a much more robust muscle in adult *A. tigrinum* (not illustrated) than it is in either *D. tenebrosus* or larval/just-metamorphosed tiger salamanders. It originates directly from the femur three-quarters of the distance to the knee and has an extensive insertion that covers approximately the distal three-quarters of the posterior border of the fibula.

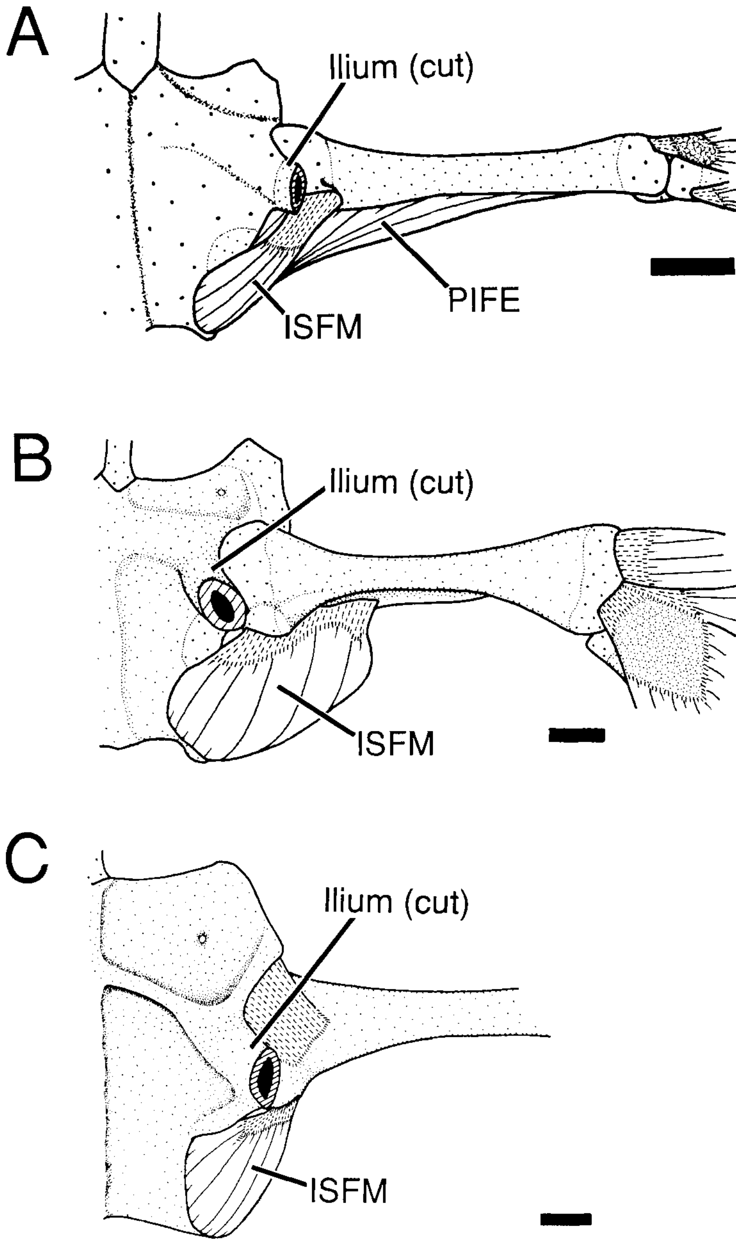

Fig. 9. Deepest dorsal pelvic musculature. The ilium has been cut and deflected outward to expose the dorsal surface of the pubo-ischiac plate. ILFB, ILFM, ILTA, ILTP, and PIFI have been removed. Right leg. **A:** *A. tigrinum*, larva, KU 89141. **B:** *A. tigrinum*, adult, UCI 17. **C:** *D. tenebrosus*, LACM 84541. Scale bars = 2 mm.

M. flexor primordialis communis (FPC)

The flexor primordialis communis arises partially via a strong tendon from the posteroventral border of the fibular condyle of the femur, and partially directly from the posteroventral face of the fibula (Figs. 1, 2A, 4A). The fibers of the FPC insert ventrally onto the plantar aponeurosis that extends via strong tendons along the digits to be anchored to the proximal ventral borders of the distal phalanges.

Variation: The plantar fascia is much more extensive in *D. tenebrosus* than in *A. tigrinum* (compare Figs. 2A,B, 4A,B), resulting in a larger surface for insertion in the former. In one *A. tigrinum* larva, a few fibers originated from a common insertion tendon of FMFB and EXF.

Dorsal femoral muscles

M. extensor cruris tibialis (EXT)

The extensor cruris tibialis originates from the dorsal border of the tibial condyle of the femur (Fig. 1) via a strong, flat tendon. Its fibers insert directly onto the dorsal surface of the distal three-quarters of the tibia and, crossing the ankle joint, onto the anterodorsal surface of the tibiale and prehallux. The EXT is a parallel-fibered muscle (Figs. 2A, 3A, 5A).

Variation: In *D. tenebrosus,* the EXT has a unipinnate origin and has a more extensive insertion on the tibia; it covers the entire anterolateral surface of the tibia to the anterior side of the base of the tibial spine (Figs. 2B, 3B, 5B).

M. extensor digitorum communis (EDC)

The extensor digitorum communis is a relatively thin, flat, fan-shaped (though not pinnately arranged) muscle arising in common with EXF from the dorsal border of the femoral condyles (Fig. 1) via a strong, thick aponeurosis. This aponeurosis typically covers the proximal portion of the muscle to varying degrees (Figs. 3A, 5A, 6A). In one larval *Ambystoma* (Fig. 6A), the anterior section of the muscle had no connection to the femur, except for a diffuse fascia, and originated solely from the insertion tendon of ILTA/ILTP, whereas the posterior section of the muscle arose from the tendon of origin in common with EXF. The insertion of the muscle is via a thin, short aponeurosis onto the dorsal surfaces of the proximal ends of the metatarsals.

Variation: In *D. tenebrosus,* EDC inserts onto tough connective tissue covering the surface of the extensores digitorum breves (Francis, '34; Figs. 3B, 5B).

M. extensor cruris et tarsi fibularis (EXF)

The extensor cruris et tarsi fibularis is a unipinnate muscle originating in common with EDC from the dorsal border of the femoral condyles via a strong, thick aponeurosis that typically covers the proximal one-quarter of the surface of the muscle. The posterior half of the muscle inserts directly onto the posterodorsal face of the fibula. (In two *Ambystoma* larvae, a few of the fibers inserted tendinously in common with the fibers of the FMFB.) The anterior half of the muscle crosses the ankle joint to insert onto the dorsal surface of the fibulare (Figs. 3, 5, 6A).

DISCUSSION

Intraspecific variation

Considerable variability in the musculoskeletal system was observed in the animals examined. For instance, one larval tiger salamander completely lacked the ILFM on one side of the pelvic girdle, whereas it was present on the other side, and another specimen lacked the crista tibialis on one leg. Possibly these variations were tolerated because the animals were still aquatic and the performance of the limbs was not yet critical. It is also possible that there is enough redundancy in the limb musculature to accommodate these deficits. These hypotheses could be tested in a crude fashion by denervation or excision of particular muscles. Certainly minor variations in muscle form can be tolerated (e.g., presence or absence of pinnation in the ISFM of *Dicamptodon,* variation in insertion of fiber clumps of PTB, PIT, ISF, ILTA). These observations of intraspecific variability should serve as a caution for researchers when attempting to characterize the myology of different species.

Comparative morphology

Interspecific myological variation also is evident (Table 1). If the condition described by Francis ('34) for *Salamandra* is used as a basis for comparison, then several trends which may be related to life-history traits in the taxa involved are apparent.

Aquatic taxa generally have reduced (*Typhlomolge*) or undifferentiated (*Cryptobranchus, Necturus*) limb musculature compared with terrestrial forms. All of the limb muscles in *Typhlomolge* (Plethodontidae; a blind cave salamander, Duellman and Trueb, '86; Emerson, '05) are extremely slender, and Emerson ('05) stated that the ILTA and ILTP are fused into one indistinguishable sheet (Table 1). As in the aquatic *Onychodactylus japonicus* (personal observation), a member of the Hynobiidae (generally accepted as the most primitive extant salamander family; Duellman and Trueb, '86), PIT in *Typhlomolge* seems to lack the tendon separating it into proximal and distal portions. ILFM originates solely from the lateral face of the ilium; the more extensive origin from the dorsal surface of the pubo-ischiac plate is missing. The ISF has also switched insertions from the more typical position on the plantar fascia seen in all other salamanders examined, including *Onychodactylus* (personal observation), to one on the proximal end of the tibia. *Necturus* (Proteidae), which prefers lakes and streams (Obst et al., '88), has more robust musculature than *Typhlomolge*. However, in *Necturus* the PIFI and ILFM are fused to form a single muscle that originates from the dorsal surface of the pubo-ischiac plate and passes around both sides of the ilium to unite and insert on the femur (Gilbert, '73, PIFI; Table 1). *Cryptobranchus* (= *Menopoma* of Mivart, 1869), a member of a salamander family (Cryptobranchidae) considered relatively primitive (Duellman and Trueb, '86), is described by Mivart (1869) as having well-developed limb musculature, which may be correlated with its preference for fast-moving streams (Obst et al., '88). However, the thigh musculature of *Cryptobranchus* is relatively undifferentiated; both the PTB and PFM are missing (Table 1), presumably having merged with PIT and PIFE, respectively. As is the case with *Typhlomolge*, the PIT apparently lacks the intramuscular tendinous sheet. Two major muscles controlling the thigh of *Cryptobranchus*, PIFE and PIFI, have an expanded insertion (and therefore a longer moment arm) in comparison with *Salamandra;* both insertions extend down the entire length of the femur to the femoral condyles (Mivart, 1869). The insertion of CPIT apparently has switched in *Cryptobranchus* from the posterior border of PIT to join ISF just lateral to the pubo-ischiac plate (Mivart, 1869). This was confirmed by Appleton ('28) and by personal observation; the functional significance of this switch is unclear. Darevsky and Salomatina ('89) observed that in a rare aquatic adult specimen of *Paramesotriton deloustali* (Salamandridae), the distally located FMFB is reduced, whereas the more proximal ISF is greatly enlarged. In *Onychodactylus* (personal observation), the CPIT forms one continuous, thick sheet with CDF, inserting partially on the PIT and partially on the femur. The FMFB is large and the ISF is a thin slip originating from the posterior surface of the PIT at the level of the acetabulum; no intramuscular tendon is evident, and it is hypothesized that only the distal portion of ISF is present in this species.

More terrestrial forms (e.g., *Ambystoma, Dicamptodon, Pseudoeurycea, Taricha*) have more strongly differentiated muscles, and many smaller, one-joint muscles are relatively robust. In *Pseudoeurycea bellii* (Baird, '51), the PFM is stout and composed of two distinct heads. In contrast to their conditions in *Cryptobranchus,* both the PIFE and PIFI in *Pseudoeurycea* insert only on the proximal portion of the femur; however, the PIFI has a long accessory tendon that extends from the anterodorsal surface of the muscle to insert on the knee capsule. The short moment arms of these one-joint hip muscles may contribute to more rapid movements of the limbs. It is interesting to note that Darevsky and Salomatina ('89) described a greatly enlarged femorofibularis and reduced ischioflexorius in adult terrestrial specimens of *Paramesotriton deloustali,* which engage in active and coordinated terrestrial locomotion. In *P. deloustali,* the large femorofibularis inserts on a pronounced crista fibularis on the posterolateral border of the fibula. Smith ('27) described just such a structure on the fibula of *Taricha torosa* (= *Triturus torosus* of Smith, '27; Salamandridae), and also stated that the femorofibularis is robust in this species, whereas the ischioflexorius is thin.

These general morphological trends observed in terrestrial and aquatic species suggest functional correlates. If an aquatic animal simply uses its limbs as paddles or struts, and has no need for finely controlled movements, it has no need for highly differentiated muscles. Moreover, the greater muscle mass located proximally on the limb (e.g., PIFE, PIFI, ISF) would contribute to moving the limb as a whole. The limbs of terrestrial forms, in contrast, must support the weight of the body and bend the joints such that limb movement is controlled accurately. Greater differentiation and greater bulk of both small and distal muscles in the limbs may have evolved in response to higher force requirements and the need for more specifically controlled movements (Schaeffer, '41).

Ontogenetic corollaries of these trends may be seen in the present study. The appearance and relative mass of the hind limb muscles of larval and just-metamorphosed tiger salamanders are indistinguishable (Ashley et al., '91). In contrast, in the two tiger salamanders that were maintained out of the water for many years, both the femorofibularis and ischiofemoralis muscles had expanded insertions (Fig. 9A,B). Moreover, both of these muscles seem to have increased in bulk relative to other limb muscles. Although this observation must be interpreted with caution due to the small sample size, the enlargement of the FMFB is suggestive of that seen in *Paramesotriton* (Darevsky and Salomatina, '89) and *Taricha* (Smith, '27). Neither Smith ('27) nor Darevsky and Salomatina ('89) describe the ischiofemoralis muscle. Experimental tests are required to determine whether or not the muscular changes seen in *A. tigrinum* are primarily dependent on use patterns or on age.

In *D. tenebrosus,* the connective tissue in the limb is much thicker and tougher than that seen in either larval or metamorphosed *Ambystoma,* and the area of aponeuroses from which muscle fibers take their origin is much larger. Although Pacific giant salamanders are good walkers, they have a reduced femorofibularis and a large ischioflexorius, exactly the opposite of the condition shown by *Paramesotriton* and *Taricha.* Francis ('34) stated that, in *Salamandra,* both the femorofibularis and distal section of the ischioflexorius are innervated by branches of the same nerve, the N. sciaticus. Thus, it is tempting to speculate that the femorofibularis and ischioflexorius muscles may represent functionally analogous systems, only one of which is required for coordinated terrestrial locomotion. This speculation will have to be tested by experimental manipulation involving denervation or excision of the relevant muscles.

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