

Postcranial Myology of the California Newt, *Taricha torosa*

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ABSTRACT

Salamanders are generally agreed to represent the primitive tetrapod body plan, as well as a postural analog for early tetrapods. Dissection and description of the muscles of the forelimb, trunk, and hindlimb of the California newt, *Taricha torosa*, were undertaken to provide baseline data on the locomotor structures in this species. Hypaxial trunk muscles are similar to those of other vertebrates. As in other salamanders, limb muscles show a simple parallel-fibered architecture and often span multiple joints. Several differences in limb musculature were also noted. The extensor iliobtibialis muscle possesses a single head in *T. torosa*, rather than the two heads common in larger salamander species. The ischioflexorius muscle, while divided into proximal and distal sections, is not distinct from the puboischiotibialis in its proximal portion. The femorofibularis is enlarged in this species; it is suggested that the femorofibularis and ischioflexorius muscles may be functionally analogous systems. Forelimb and hindlimb musculature show similar morphological patterns, particularly in distal limb segments, which may provide insight into the primitive arrangement of tetrapod limb muscles. © 2005 Wiley-Liss, Inc.

Key words: salamander; amphibian; musculature; hindlimb; forelimb; trunk

Salamanders have traditionally been of interest to comparative anatomists, as they are thought to represent the basic tetrapod body plan; generations of comparative anatomy students have dissected *Necturus* as part of their studies. Indeed, salamanders are generally agreed to be the closest extant postural model for early tetrapods (Edwards, 1977, 1989) and salamander anatomy has been essentially unchanged for at least the last 150 million years (Gao and Shubin, 2001). A number of researchers in the field of biologically inspired robotics have turned to the salamander as their model of choice in trying to build a robot capable of coordinated autonomous locomotion (Ijspeert, 2000, 2001; Taylor and Massey, 2001; Breithaupt et al., 2002).

Given this seemingly central position in vertebrate anatomy and current interest in salamander locomotor systems, it is lamentable that relatively few careful descriptions of salamander musculature are available. From the standpoint of comparative anatomy, little appreciation has been given to divergence from the pattern seen in *Necturus* (Gilbert, 1973), even though aquatic versus terrestrial habits may put different demands on the musculoskeletal system. From the standpoint of biomechanics and biomimetics, in order to understand how muscles and bones interact to produce locomotion, it is necessary to

determine when muscles are active, usually by the technique of electromyography (EMG). For EMG studies to be successful, it is necessary to have an accurate understanding of muscular anatomy to guide electrode implantation.

In this study, we describe the postcranial muscular morphology of the California newt. Newts comprise a subgroup of salamanders with the specific characteristic of possessing a terrestrial juvenile stage, termed the eft. Adults return to the water to breed and may become secondarily aquatic, often developing a pronounced dorsal crest and tail fin (Petranka, 1998). The California newt, *Taricha torosa*, follows this pattern, but adults do not develop crest or fin. Indeed, California newts migrate long

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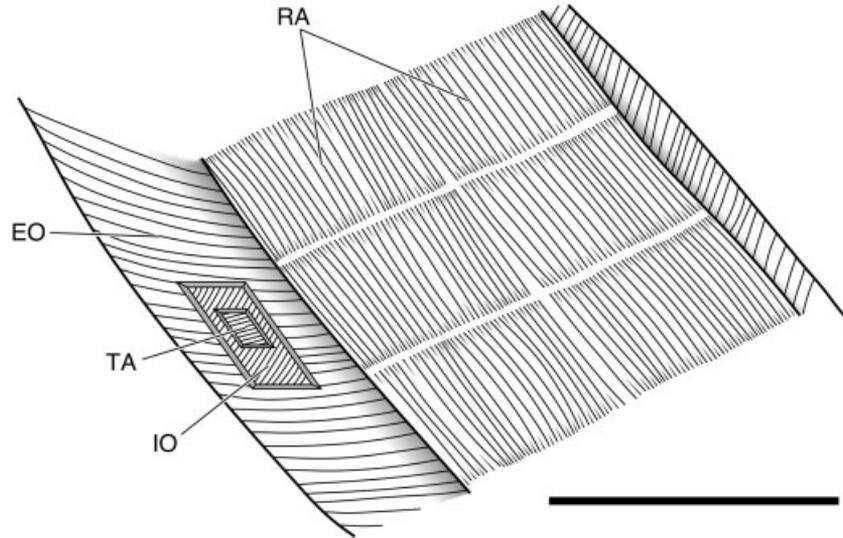


Fig. 1. Section of trunk musculature. Anterior is toward the upper left. In this and the following figures, the attachments of the muscles are designated by the small triangular hash marks at the ends of the fibers, tendon is white and its attachments are indicated by short dashes, bone is indicated by fine stippling, and cartilage by coarse stippling. Scale bar = 1 cm.

distances annually (in some areas, roads are closed to protect newts crossing them in mass numbers during the breeding season) and thus maintain a primarily terrestrial existence, though they may be found walking along the bottom of streams. They are thus capable of locomotion in environments that pose differing requirements for support, though quadrupedal walking may be used in both.

This anatomical study has two general goals. First, it provides baseline morphological data for an examination of the neuromuscular basis of newt locomotion in different environments. Second, it represents a contribution to our understanding of comparative morphology of urodeles and synonymizes the forelimb muscles described with terms given by previous workers.

MATERIALS AND METHODS

Four formalin-fixed specimens of *Taricha torosa* (Rathke, 1833) were dissected in this study; all were collected in Orange County, California. Dissections were performed with a Zeiss Stemi 11V microscope outfitted with a camera lucida. An iodine stain (Bock and Shear, 1972) was periodically applied during dissections to better distinguish fiber direction and connective tissue. Tracings made using the camera lucida were imported into a Macintosh Power PC computer using a Wacom drawing tablet (Wacom Technology, Vancouver, WA), and the anatomical figures were detailed and finished using Canvas 8 (ACD Systems, Miami, FL).

Abbreviations

The following abbreviations are used for muscle names: AbD5, abductor digiti V; AbED1, abductor et extensor digiti I; AC, anconaeus coracoideus; AHL, anconaeus humeralis lateralis; AHM, anconaeus humeralis medialis; ASM, anconaeus scapularis medialis; C, cucullaris; CBL, coracobrachialis longus; CCL, contrahentium caput lon-

gum; CD, contrahentes digitorum; CDF, caudofemoralis; CLMC, caput longum musculorum contrahentium; CPIT, caudalipuboischiotibialis; DS, dorsalis scapulae; EACR, extensor antebrachii et carpi radialis; EACU, extensor antebrachii et carpi ulnaris; ECT, extensor cruris tibialis; ECTF, extensor cruris et tarsi fibularis; EDB, extensores digitorum breves; EDC, extensor digitorum communis; ELD4, extensor lateralis digiti IV; EO, obliquus externus; ETT, extensor tarsi tibialis; FACR, flexor antebrachii et carpi radialis; FACU, flexor antebrachii et carpi ulnaris; FAL, flexor accessorius lateralis; FAM, flexor accessorius medialis; FBP, flexores breves profundi; FBS, flexores breves superficiales; FDC, flexor digitorum communis; FMFB, femorofibularis; FPC, flexor primordialis communis; HAB, humeroantebrachialis; ILC, iliocaudalis; ILFB, iliofibularis; ILT, extensor iliotibialis; IMC, intermetacarpales; IMT, intermetatarsales; IO, obliquus internus; IOC, interosseus cruris; ISC, ischiocaudalis; ISF, ischioflexorius; LD, latissimus dorsi; O, opercularis; P, pectoralis; PCH, procoracohumeralis; PFM, pubifemoralis; PIFE, puboischiofemoralis externus; PIFI, puboischiofemoralis internus; PIT, puboischiotibialis; PP, pronator profundus; PTB, pubotibialis; RA, rectus abdominis; SC, supracoracoideus; TA, transversus abdominis

RESULTS

For each of the muscles described below, the anatomical arrangement is followed by a statement on function. For muscles in which the activity periods have been described by electromyography in other species, the reference is given. All other functions are presumed (and listed as such), as they have not been tested experimentally.

Muscles of Abdomen

M. rectus abdominis (RA; Fig. 1). This muscle is the most superficial of the trunk muscles. It is divided into superficial and deep portions; both originate on the ante-

rior border of the pubo-ischiac plate and ypsiloid cartilage. Right and left halves of the muscle are separated down the midline by an aponeurosis, the linea alba. Segments of the muscle are divided by a series of tendinous inscriptions. The fibers are arranged in parallel and run longitudinally. The superficial portion of the muscle inserts on the sternal cartilage, the pericardium, and the *M. pectoralis* (for the lateral fibers). There is also a slip that is continuous with the *M. rectus cervicis superficialis* (not illustrated), which inserts on the first ceratobranchial. The deep portion of the muscle is continuous with the *M. rectus cervicis profundus* (not illustrated), which runs anteriorly to insert on the hyoid. Presumed function: prevent sagging of the trunk during walking, draw the pelvic and pectoral girdles ventrally toward each other.

M. ypsiloideus (not illustrated). This muscle appears to be the posterior continuation of the portion of the superficial RA that spans the area between the ypsiloid cartilage and the pelvic girdle. Formally, it originates on the anterior edge of the medial pubis and inserts on the arms of the ypsiloid cartilage. Presumed function: assist the RA in preventing sagging of the trunk.

M. obliquus externus (EO; Fig. 1). The external oblique muscle forms the superficial layer of the lateral trunk musculature. It is parallel-fibered; the fibers run diagonally from dorsoanterior to ventroposterior, making an angle of approximately 50° with the body axis (where 0° would be directed toward the head and 180° would be directed toward the tail). This muscle originates on the epaxial muscular fascia, and the two sides are inserted into an aponeurosis that crosses the midline, deep to the RA. Function: oppose long-axis torsion generated by limb support during walking and bend the body during swimming (Carrier, 1993; Bennett et al., 2001).

M. obliquus internus (IO; Fig. 1). The thin *m. obliquus internus* lies deep to the EO. The fibers of this muscle run in a nearly perpendicular direction to those of the EO: obliquely from ventroanterior to dorsoposterior, making an angle of approximately 145° with the body axis. It originates from connective tissue deep to the EO and inserts on an aponeurosis that crosses the midline. Function: oppose long-axis torsion generated by limb support during walking and bend the body during swimming (Carrier, 1993; Bennett et al., 2001).

M. transversus abdominis (TA; Fig. 1). Under both of the oblique muscles is the *m. transversus abdominis*. The fibers of this very thin muscle run in a dorsoventral direction. This muscle attaches to the transverse processes of the trunk vertebrae and crosses the midline to attach on the other side. Function: oppose long-axis torsion generated by limb support during walking and bend the body during swimming (Carrier, 1993; Bennett et al., 2001); power exhalation during respiration (Brainerd, 1999).

Muscles of Hindlimb

Muscles originating on the caudal vertebrae are as follows.

M. ischiocaudalis (ISC; Fig. 2). This is the most medial of the three ventral muscles that connect the tail and pelvic girdle/hindlimb. It originates from the trans-

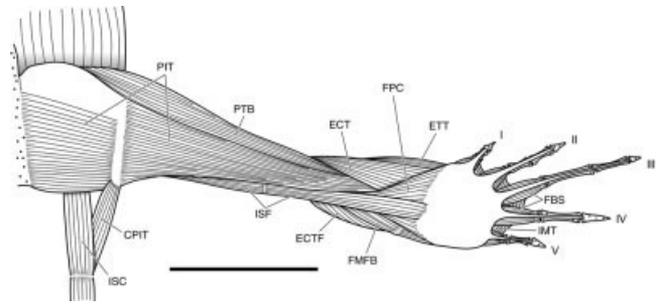


Fig. 2. Superficial musculature of the hindlimb, ventral view. Anterior is toward the top of the figure. Digits are indicated by Roman numerals. Scale bar = 1 cm.

verse process of the fourth caudal vertebra and inserts on the posterior border of the ischium. It is a very flat and thin strap-like muscle with parallel fibers. Presumed function: draw the tail laterally.

M. caudalipuboischiotibialis (CPIT; Fig. 2). This muscle is just lateral to the ISC and, like the ISC, has a parallel-fibered architecture. It also originates from the transverse process of the fourth caudal vertebra. However, this muscle's tendon of insertion does not connect to bone, but rather to the tendinous inscription dividing the proximal and distal portions of the PIT. Function: assist the PIT in limb retraction and flexion of the tail laterally (Ashley-Ross, 1995).

M. caudofemoralis (CDF; Figs. 3 and 4). The strap-like CDF is located deep to the CPIT. It originates on the transverse processes of the fourth and fifth caudal vertebrae and inserts via a strong tendon onto the crista ventralis of the femur. Function: retract the femur (Ashley-Ross, 1995).

M. iliocaudalis (ILC; Fig. 3). This parallel-fibered muscle originates from the first several caudal vertebrae and inserts on the ilium. The fibers of the muscle run parallel to the epaxial muscles, and it is only distinguishable from them by its insertion. Presumed function: draw the tail laterally.

Muscles originating on the ventral pelvic girdle are as follows.

M. puboischiotibialis (PIT; Figs. 2 and 3). This parallel-fibered muscle can be seen from a ventral view as the most superficial muscle over the pelvis. It originates on the pubo-ischiac plate lateral to the midline. It is divided into well-defined proximal and distal sections by a tendinous inscription at approximately the level of the acetabulum. It narrows as it passes down the leg to insert on the anterior surface of the tibia. Function: support the body during walking, retract the femur and flex the knee (Ashley-Ross, 1995).

M. pubotibialis (PTB; Figs. 2 and 3). The PTB originates from the anterior edge and anterior ventral face of the pubo-ischiac plate. Its parallel fibers pass anterior to the PIT and insert on the anterior face of the proximal end of the tibia. Function: support the body during walking and flex the knee (Ashley-Ross, 1995).

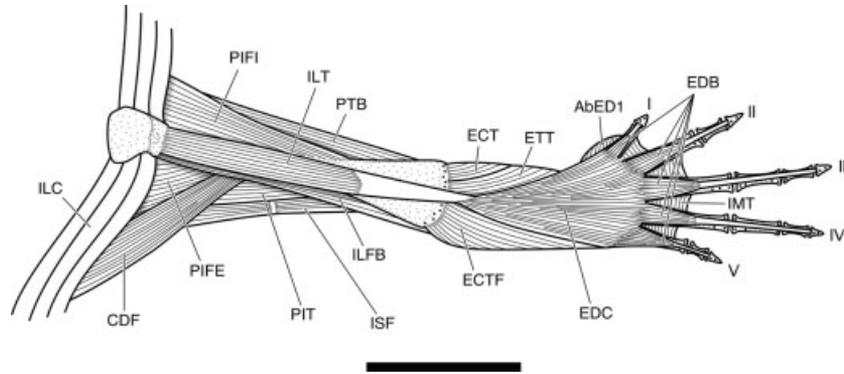


Fig. 3. Superficial musculature of the hindlimb, dorsal view. Anterior is toward the top of the figure. Digits are indicated by Roman numerals. Scale bar = 1 cm.

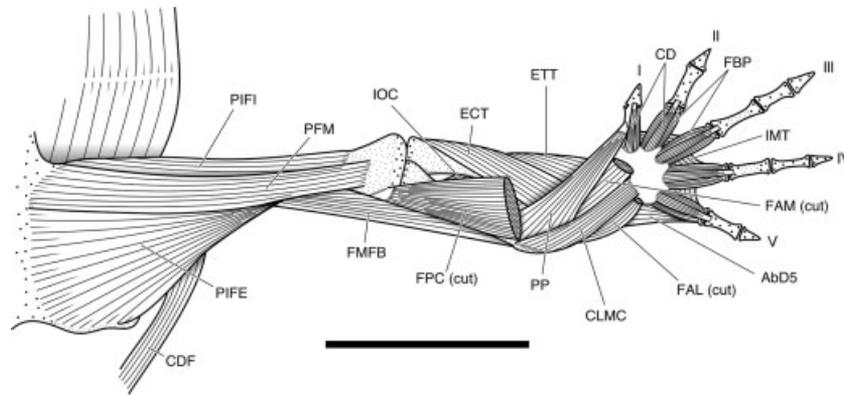


Fig. 4. Deep musculature of the hindlimb, ventral view. Anterior is toward the top of the figure. Digits are indicated by Roman numerals. Scale bar = 1 cm.

M. ischioflexorius (ISF; Figs. 2 and 3). This muscle originates from the posterior and lateral edge of the ischium behind the PIT. It is parallel-fibered and, like the PIT, divided into distinct proximal and distal portions by a tendinous inscription. However, the proximal section is incompletely divided from the PIT; it is possible to see what seems to be the division between muscles, but mechanical separation is difficult. Only the distal portion is completely separate from the PIT. It inserts on the plantar aponeurosis overlying the flexor primordialialis communis. Function: assist in limb retraction (Ashley-Ross, 1995).

M. puboischiofemoralis externus (PIFE; Figs. 3 and 4). This fan-shaped muscle originates from much of the ventral surface of the pubo-ischiac plate and crosses the hip joint to insert on the ventral surface of the femur. The insertion on the femur is extensive, covering nearly two-thirds of the length of the ventral surface of the bone. Function: support the body during walking and retract the femur (Ashley-Ross, 1995).

M. pubifemoralis (PFM; Fig. 4). The PFM is the anteriormost of the ventral deep muscles of the thigh. It originates from the anterior and ventral surface of the pubo-ischiac plate anterior to the PIFE. It inserts on the ventral face of the femur both anterior and distal to the insertion of the PIFE but posterior to the m. pubois-

chiofemoralis internus (PIFI). Function: support the body during walking and retract the femur (Ashley-Ross, 1995).

M. ischiofemoralis (not illustrated). This short muscle spans the hip joint, originating on the lateral border of the ischium (the posterior portion of the pubo-ischiac plate), and inserting on the posterior face of the head of the femur. Presumed function: retract the femur.

Muscles originating on the dorsal pelvic girdle are as follows.

M. puboischiofemoralis internus (PIFI; Figs. 3 and 4). The PIFI originates from the internal (dorsal) face of the pubo-ischiac plate. It passes anterior to the ilium, crossing the hip joint and inserting extensively on the femur (covering the anterior face, as well as extending dorsally and ventrally), anterior to the insertion of the PIFE. Function: protract and elevate the femur (Ashley-Ross, 1995).

M. extensor iliotibialis (ILT; Fig. 3). This strap-like, parallel-fibered muscle originates from the lateral surface of the ilium above the acetabulum. It crosses the hip and knee joints to insert via a long strong tendon on the spine of the tibia. Function: extend the knee joint (Ashley-Ross, 1995).

M. iliofibularis (ILFB; Fig. 3). The ILFB originates from the external face of the ilium just posterior to the ILT. It courses parallel to, but slightly deep and posterior to, the ILT, crossing both hip and knee joints to insert via a tendon on the posterior side of the proximal end of the fibula. Function: elevate the femur and flex the knee joint (Ashley-Ross, 1995).

Muscles originating on the femur are as follows.

M. extensor cruris tibialis (ECT; Figs. 2–4). This muscle originates from the tibial epicondyle of the femur. It can be seen from both ventral and dorsal views, as it fans out from its origin to cover much of the anterior face of the tibia, with expansions onto the dorsal and ventral faces of that bone. It inserts extensively on anterodorsal and anteroventral faces of the tibia. Presumed function: extend the knee joint (tibia).

M. extensor tarsi tibialis (ETT; Figs. 3 and 4). This muscle originates from the tibial epicondyle of the femur next to the ECT. The muscle fibers run parallel to the ECT and insert on the ventral surface of the tibia bone. Presumed function: supinate the foot.

M. extensor cruris et tarsi fibularis (ECTF; Figs. 2 and 3). The ECTF originates from the fibular epicondyle of the femur and, complementary to the ECT, inserts on much of the posterodorsal and posteroventral faces of the fibula. A portion of the muscle inserts on the fibulare. Presumed function: extend the knee joint (fibula).

M. femorofibularis (FMFB; Figs. 2 and 4). This strap-like, parallel-fibered muscle originates from the ventral face of the distal end of the femur. It inserts on the posterolateral face of the fibula. Unlike many other salamander species studied, the FMFB is a fairly robust muscle in *T. torosa*. Function: flex the knee joint (Ashley-Ross, 1995).

M. flexor primordialialis communis (FPC; Figs. 2 and 4). The bulk of the FPC originates from the posteroventral face of the fibula, though part of it arises via a tendon from the fibular epicondyle of the femur. The fibers run ventrally and insert onto the plantar aponeurosis (plantar fascia). The large aponeurosis extends over the ventral surface of the foot and divides into five tendons that insert on the proximal end of the terminal phalanx of each digit. Function: press the plantar surface of the foot firmly against the ground during walking (Ashley-Ross, 1995).

M. extensor digitorum communis (EDC; Fig. 3). The thin EDC is located on the dorsal surface of the crus between the ETT and ECTF. It originates mostly from the lateral epicondyle of the femur anterior to the ECTF, but may also demonstrate a small number of fibers arising from the tibial spine. The fibers of the EDC fan out to insert on the bases of the metatarsals by many small tendons. Presumed function: extend the knee joint and abduct the foot.

Muscles of the crus and foot are as follows.

M. interosseus cruris (IOC; Fig. 4). This muscle joins the medial sides of the tibia and fibula. It arises from the proximal part of the fibula and inserts on the distal

portion of the tibia. Presumed function: stabilize the two long bones of the crus.

M. flexor accessorius lateralis (FAL; Fig. 4). The FAL originates from the lateral edge of the fibulare and inserts on the dorsal side of the plantar fascia. The fibers follow a diagonal course toward the anterior side of the foot. Presumed function: pronate the foot.

M. flexor accessorius medialis (FAM; Fig. 4). This muscle originates from the distal region of the fibula, the fibulare, and intermedium. It inserts on the plantar fascia, similar to the FAL. The muscle fibers run parallel to those of the FAL. Both the FAM and the FAL are parallel-fibered and generally strap-like in appearance. Presumed function: pronate the foot.

M. pronator profundus (PP; Fig. 4). This deep flexor muscle of the foot is roughly triangular in shape. It originates from the medial side of the fibula, and its fibers converge to insert on the lateral face of the distal end of the tibia, tibiale, and the base of the first metatarsal. Presumed function: pronate the foot.

M. caput longum musculorum contrahentium (CLMC; Fig. 4). The CLMC is a thin muscle that lies deep to the plantar fascia. It originates from the distal portion of the fibula on the medial side. The fibers insert on a flat tendon that attaches to the distal tarsal bones. Presumed function: flex (depress) the tarsus.

Mm. flexores breves superficiales (FBS; Fig. 2). These small muscles originate from the dorsal side of the plantar fascia. They have a complicated insertion pattern; for all digits except digit I, the muscles are tripartite, with the lateral portions inserting on the ventral side of the distal ends of the metatarsals, and the medial portion inserting on the ventral surface of the proximal end of the proximal phalanx (this connection is hidden under the extensions of the plantar fascia in Fig. 4). For digit I, the insertion is on the distal end of its associated metatarsal, without connection to the phalanx. Presumed function: flex the digits.

Mm. intermetatarsales (IMT; Figs. 2–4). These muscles form the web-like structures between the digits. They attach the metatarsals of adjacent digits. They extend further distally on the fibular side of each metatarsal. Presumed function: adduct the metatarsals and the attached digits.

Mm. contrahentes digitorum (CD; Fig. 4). These small muscles originate from the flat tendon of the CLMC as well as the tarsal bones. They pass from the tarsal bones along the ventral axis of the metatarsals to insert on the proximal phalanx of each digit. Presumed function: flex the digits.

M. abductor digiti V (AbD5; Fig. 4). The AbD5 arises from the ventral surface of the distal end of the fibula. It has an extensive insertion, making a fleshy attachment to the posterior side of the fibulare, basale V, and the base of the fifth metatarsal. Presumed function: abduct the fifth metatarsal.

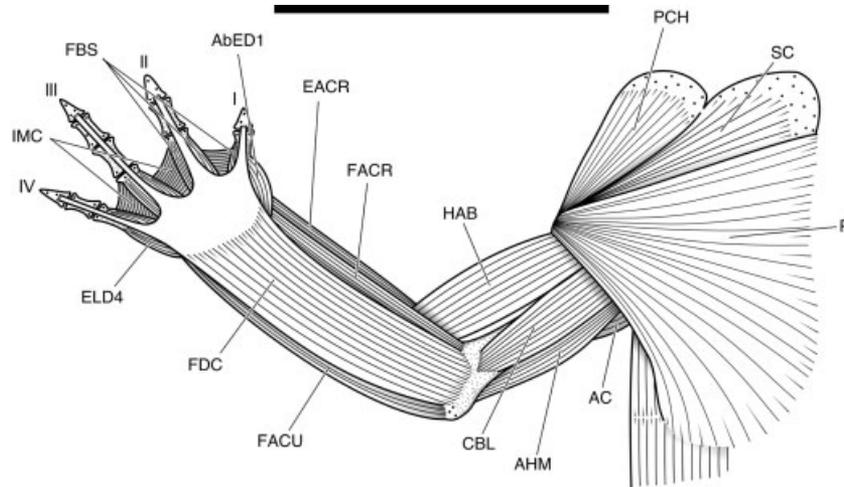


Fig. 5. Superficial musculature of the forelimb, ventral view. Anterior is toward the top of the figure. Digits are indicated by Roman numerals. Scale bar = 1 cm.

Mm. extensores digitorum breves (EDB; Fig. 3). These extensor muscles of the digits are a series of five slips, each of which originates from the distal tarsal bones at the base of its respective digit and inserts on the dorsal surface of the proximal end of its terminal phalanx via a long tendon. The muscular portion only extends to approximately two-thirds of the length of the metatarsal; the tendon continues to the terminal phalanx of the digit. Presumed function: extend the digits.

M. abductor et extensor digiti I (AbED1; Fig. 3). The AbED1 originates from the intermedium and centrale bones of the wrist. Its insertion is on the lateral face of the metatarsal and the phalanx via a small slip. Presumed function: abduct and extend the first metatarsal and its associated digit.

Muscles of Forelimb

Muscles connecting the skull and pectoral girdle are as follows.

M. opercularis (O; Fig. 6). The strap-like opercularis originates from the cartilaginous operculum associated with the otic capsule. Its fibers course parasagittally to insert on the anterior edge of the cartilaginous suprascapula. Presumed function: conduct sound, dampen movements of the operculum caused by head motion.

M. cucullaris (C; Fig. 6). The cucullaris muscle is composed of two heads: anterior and posterior. Both heads arise together from the dorsal fascia and posterior surface of the skull. The heads diverge as they pass posteriorly; the anterior, larger head inserts on the lateral surfaces of the procoracoid and scapula between the procoracohumeralis and the dorsalis scapulae, while the fibers of the posterior head run ventrally to insert on the anterolateral border of the scapula. Presumed function: turn or depress the head.

Muscles originating on the ventral pectoral girdle are as follows.

M. pectoralis (P; Fig. 5). The pectoralis is the most superficial ventral chest muscle. It is fan-shaped, with the fibers converging to insert on the crista ventralis of the humerus. The muscle has a varied origin, with some of the fibers arising from the aponeurosis that separates the right and left sides of the pectoralis, some arising from the sternum, and the posteriormost fibers taking their origin from tendinous inscriptions of the rectus abdominis. Presumed function: adduct and retract the humerus and support the weight of the body on the forelimb.

M. supracoracoideus (SC; Fig. 5). The SC originates from the ventral superficial surface of the coracoid cartilage. Its posterior portion lies deep to the P. The muscle is fan-shaped and parallel-fibered; it inserts via a flat tendon on the crista ventralis of the humerus, adjacent to the insertion of the pectoralis. Presumed function: adduct the humerus and support the weight of the body on the forelimb.

M. procoracohumeralis (PCH; Figs. 5 and 6). This muscle is the most anteriorly located of the muscles joining the pectoral girdle to the humerus. It originates from the procoracoid cartilage and inserts on the anterior surface of the proximal humerus. Presumed function: protract the humerus.

M. coracobrachialis longus (CBL; Fig. 5). The CBL arises from the posterolateral surface of the coracoid. It is a parallel-fibered muscle whose fibers run along the axis of the humerus and insert on the medial face of the distal end of that bone. Presumed function: retract the humerus.

M. anconaeus coracoideus (AC; Fig. 5). This muscle originates via a long tendon from the coracoid and extends down the posterior side of the upper forelimb, where it unites with m. anconeus scapularis medialis near the middle of the humerus. The joined muscles insert on the olecranon process of the ulna. Presumed function: extend the elbow joint.

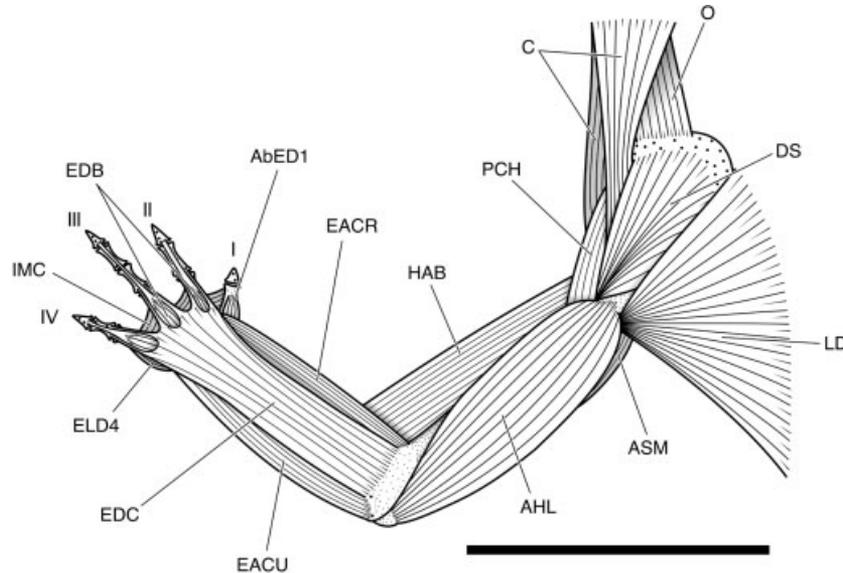


Fig. 6. Superficial musculature of the forelimb, dorsal view. Anterior is toward the top of the figure. Digits are indicated by Roman numerals. Scale bar = 1 cm.

Muscles originating on the dorsal pectoral girdle are as follows.

M. latissimus dorsi (LD; Fig. 6). The LD is a fan-shaped, flat, triangular muscle that is the largest of the dorsal shoulder muscles. It originates from dorsal fascia and the fibers converge to insert on the posterior surface of the crista ventralis of the humerus via a strong tendon. Presumed function: retract the humerus.

M. dorsalis scapulae (DS; Fig. 6). The dorsalis scapulae is another fan-shaped muscle joining the pectoral girdle and the humerus. It originates from the dorso-lateral surface of the suprascapular cartilage; the fibers pass around the anterior side of the humerus to insert on the crista ventralis of the humerus. Presumed function: elevate the humerus.

M. anconaeus scapularis medialis (ASM; Fig. 6). The ASM arises from the scapula posterior to the glenoid fossa and also from the connective tissue surrounding the joint capsule. Its parallel fibers run down the posterior side of the humerus and insert on the olecranon process. Approximately midway along the humerus, the fibers of the ASM are joined by those of the AC. Presumed function: extend the elbow joint.

Muscles originating on the humerus are as follows.

M. humeroantibrachialis (HAB; Figs. 5 and 6). This is a thick parallel-fibered muscle that arises from the anterior surface of the proximal end of the humerus. It crosses the elbow joint to insert on the proximal end of the radius. Presumed function: flex the elbow joint.

M. anconaeus humeralis lateralis (AHL; Fig. 6). The AHL is the most superficial upper forelimb muscle from a dorsal view. It originates from the proximal two-

thirds of the lateral face of the humerus and inserts on the olecranon process of the ulna. Presumed function: extend the elbow joint.

M. anconaeus humeralis medialis (AHM; Fig. 5). This final member of the anconaeus group lies along, and arises from, the entire posterior face of the humerus. Like the other anconaeus muscles, it inserts on the olecranon process of the ulna. Presumed function: extend the elbow joint.

M. flexor digitorum communis (FDC; Figs. 5 and 7). This thin muscle originates from the medial epicondyle of the humerus. The fibers run parallel to the direction of the radius and ulna and insert on a flat tendon that fills the entire palm region, the palmar fascia. The fascia continues as four small tendons that run over the ventral surface of the metacarpals and phalanges and finally attaches to the proximal end of the distal phalanx of each digit. Presumed function: flex the carpus and digits.

M. flexor antebrachii et carpi radialis (FACR; Figs. 5, 7, and 8). The FACR is the most anterior flexor muscle of the forearm, originating from the proximal portion of the medial epicondyle of the humerus. It is overlain, and thus obscured, for much of its length by the FDC. It inserts extensively on the anterior face of the radius, with a small portion of the muscle crossing the wrist joint to insert on the radiale. Presumed function: flex the carpus and pronate the forearm.

M. flexor antebrachii et carpi ulnaris (FACU; Figs. 5 and 7). This muscle is the mirror image of the FACR. It arises from the distal portion of the medial epicondyle of the humerus, and it inserts on much of the posterior edge of the ulna. A slip of the muscle crosses the wrist joint to insert on the lateral faces of the ulnare and intermedium. Presumed function: flex the carpus and supinate the forearm.

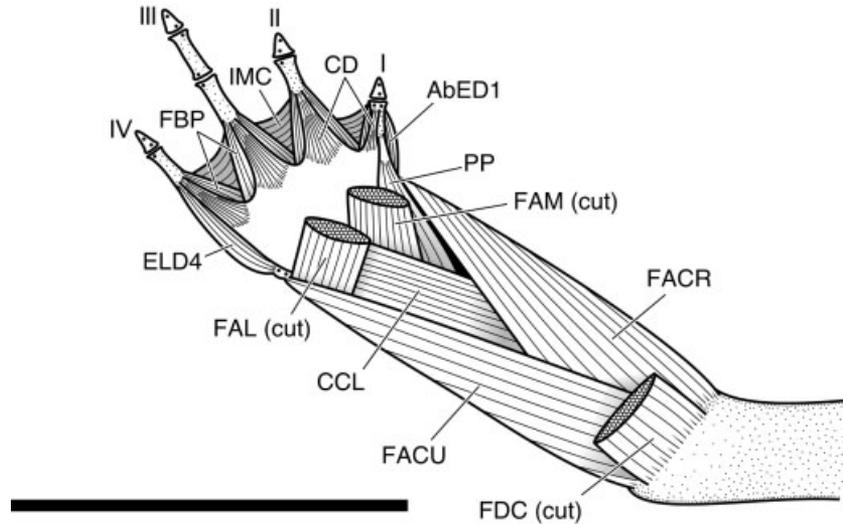


Fig. 7. Deep musculature of the forearm, ventral view. Anterior is toward the top of the figure. Digits are indicated by Roman numerals. Scale bar = 1 cm.

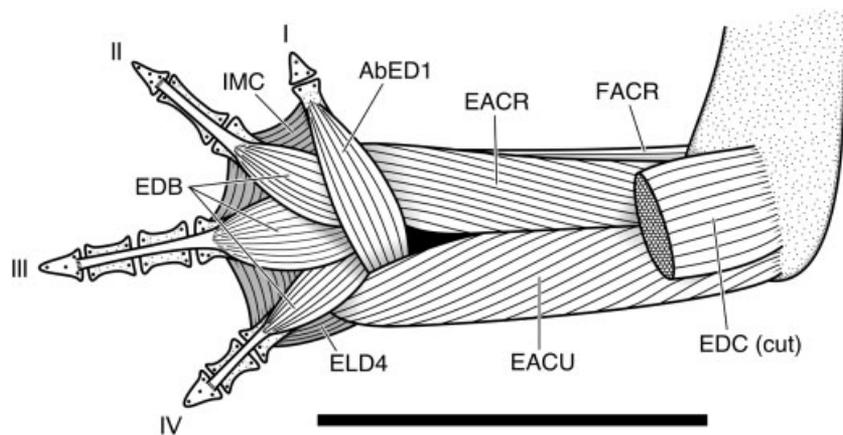


Fig. 8. Deep musculature of the forearm, dorsal view. Anterior is toward the top of the figure. Digits are indicated by Roman numerals. Scale bar = 1 cm.

M. extensor digitorum communis (EDC; Figs. 6 and 8). The EDC is the most superficial of the forearm muscles from a dorsal view. It is a thin parallel-fibered muscle that originates from the lateral epicondyle of the humerus. It inserts on the dorsal surfaces of the proximal phalanges of digits II, III, and IV via paired tendons. Presumed function: extend the carpus and digits.

M. extensor antebrachii et carpi radialis (EACR; Figs. 5, 6, and 8). The EACR lies deep, and slightly anterior, to the EDC. It arises from the proximal part of the lateral epicondyle of the humerus and inserts on almost the entire anterolateral surface of the radius and also on the lateral surface of the radiale. Presumed function: extend the carpus and forearm.

M. extensor antebrachii et carpi ulnaris (EACU; Figs. 6 and 8). This muscle mirrors the EACR; it is the posteriormost extensor muscle of the forearm and is par-

tially covered by the EDC. It arises from the distal portion of the lateral epicondyle of the humerus and inserts on the posterolateral face of the ulna, as well as on the ulnare and intermedium. Presumed function: extend the carpus and forearm.

Muscles of the forearm and hand are as follows.

M. contrahentium caput longum (CCL; Fig. 7). The strap-like CCL originates on the internal surface of the ulna and on fascia connecting the radius and ulna. It inserts on an extensive tendon that connects the carpal bones. Presumed function: flex the carpus.

M. flexor accessorius lateralis (FAL; Fig. 7). This is a simple parallel-fibered, strap-like muscle that lies deep to FDC. It originates from the distal end of the ulna, as well as the ulnare and intermedium. The fibers run diagonally toward the radius and first digit, as well as ventrally, to insert on the dorsal surface of the palmar

fascia. Presumed function: assist in flexing the metacarpals and digits.

M. flexor accessorius medialis (FAM; Fig. 7). Like the FAL, this muscle has a simple strap-like architecture and inserts on the dorsal side of the palmar fascia. The origin of the FAM is somewhat more extensive than that of the FAL, however, being approximately the distal third of the ulna, as well as the ulnare and intermedium. Presumed function: assist in flexing the metacarpals and digits.

M. pronator profundus (PP; Fig. 7). This very deep muscle originates from the medial side of the ulna, the ulnare, and intermedium. The PP crosses to the radial side of the wrist and inserts on the radiale and the base of the first metacarpal. Presumed function: pronate the hand.

Mm. flexores breves superficiales (FBS; Fig. 5). These small muscles originate from the dorsal surface of the palmar fascia and insert on the lateral edges of the distal ends of the metacarpals. For digits II and III, slips of the FBS are present on both sides of the metacarpals. For digits I and IV, however, the FBS is only seen on the medial side of the metacarpal. Presumed function: flex the digits.

Mm. intermetacarpales (IMC; Figs. 5–8). The intermetacarpales muscles are roughly triangular in shape and connect adjacent metacarpals. They originate on the radial side of each digit's metacarpal bone and insert on the ulnar side of the adjacent digit's metacarpal. Presumed function: adduct adjacent metacarpals and their associated digits.

Mm. extensores digitorum breves (EDB; Figs. 6 and 8). These short muscles connect the carpal bones with the phalanges. They originate from the carpals at the bases of digits II, III, and IV and insert via long tendons on the dorsal surface of the proximal end of the corresponding digit's terminal phalanx. Presumed function: extend the digits.

M. abductor et extensor digiti I (AbED1; Figs. 5–8). The AbED1 originates from the radiale and intermedium bones of the wrist and inserts on the distal end of the first metacarpal. Presumed function: abduct and extend the first metacarpal and its associated digit.

M. extensor lateralis digiti IV (ELD4; Figs. 5–8). The ELD4 is a very small muscle that originates from the ulnare and intermedium and inserts on the lateral edge of the fourth metacarpal. Presumed function: abduct and extend the fourth metacarpal and its associated digit.

Mm. contrahentes digitorum (CD; Fig. 7). These short muscles lie deep to the tendons of insertion of the FBS. They originate partly from the tendon that is the insertion of the CCL and partly from the carpals. The CDs insert on the proximal end of the proximal phalanx of each digit. Presumed function: flex the digits.

Mm. flexores breves profundi (FBP; Fig. 7). These deep small muscles originate from the carpals at the bases of their respective digits. They insert primarily on the metacarpal, but also on the proximal end of the proximal phalanx, of each digit. Presumed function: flex the metacarpals and their associated digits.

DISCUSSION

Overall, the trunk and limb musculature of *Taricha torosa* is similar to that of other primarily terrestrial salamander species studied (e.g., Francis, 1934; Ashley-Ross, 1992). Table 1 presents a synonymy of forelimb muscles in different salamander species. For trunk and hindlimb muscles, equivalent tables are presented in Simons and Brainerd (1999) and Ashley-Ross (1992), respectively. Hypaxial trunk muscles follow the typical vertebrate pattern of three obliquely oriented layers along with a superficial rectus abdominis (Fig. 1). Most muscles in both the forelimb and hindlimb are gracile, with simple parallel-fibered, strap-like architecture. Hindlimbs differ from forelimbs in that the major muscles cross multiple joints and thus may be capable of complex actions during locomotion.

While basic similarity of myology among salamander species is evident, there are nonetheless several specific differences, particularly in the hindlimb, that are worth noting. For instance, Francis (1934) and Mivart (1869) describe the PIT in *Salamandra* and *Cryptobranchus* (previously called *Menopoma*), respectively, as a continuous sheet of muscle, without a division into proximal and distal portions. The CPIT is inserted into the posterior border at approximately the level of the acetabulum by means of a tendon, but the tendinous inscription seen in *Taricha*, *Ambystoma*, and *Dicamptodon* (Ashley-Ross, 1992) at that location is lacking. It is unclear what functional significance this difference may have; Ashley-Ross (1995) showed in *Dicamptodon* that the PIT and CPIT are coactive during walking, suggesting that passive resistance to tension that would be afforded by tendon is not an issue.

Interestingly, the present observation of a lack of differentiation into anterior and posterior sections of the extensor iliotibialis muscle is at odds with Smith's (1927) findings on a closely related species, *Taricha granulosa* (at that time named *Triturus torosus*). Smith (1927) described *T. granulosa* as possessing two distinct parts of this muscle, which she named the rectus femoris and glutaeus maximus. The presence or absence of division of the extensor iliotibialis into two separate parts varies among salamanders previously studied; many have a distinct pars anterior and pars posterior of this muscle [e.g., *Cryptobranchus* (Mivart, 1869); *Salamandra* (Francis, 1934); *Pseudoeurycea* (Baird, 1951); *Necturus* (Gilbert, 1973); *Ambystoma* and *Dicamptodon* (Ashley-Ross, 1992)], though other groups have a single sheet of muscle [e.g., *Amphiuma* (Davison, 1895); *Typhlomolge* (Emerson, 1905); *Bolitoglossa* (Restrepo and Hoyos, 1998)]. Whether or not a particular species has one or two parts of this muscle may depend on limb proportions: those species possessing two heads of the muscle (*Cryptobranchus*, *Necturus*, *Salamandra*, *Pseudoeurycea*, *Ambystoma*, *Dicamptodon*) have robust limbs with relatively large muscles, while those having only one head of the extensor iliotibialis (*Amphiuma*, *Typhlomolge*, *Bolitoglossa*, *Taricha*) have relatively slender limbs and muscles. Aquatic versus terrestrial habits do not seem to dictate the form of the muscle(s), as *Cryptobranchus*, *Necturus*, *Amphiuma*, and *Typhlomolge* are all exclusively aquatic (Mivart, 1869; Emerson, 1905; Obst et al., 1988), yet they differ in the form of the extensor iliotibialis. Similarly, *Salamandra*, *Pseudoeurycea*, *Ambystoma*, *Dicamptodon*, *Bolitoglossa*, and *Taricha* are all primarily terrestrial (Obst et al., 1988; Petranka, 1998); the latter two species have a single head of the extensor iliotibialis, while the others have two.

TABLE 1. Synonymy of salamander forelimb muscles described for various genera.

Muscle ^a	Francis (1934) ^b <i>Salamandra</i>	Davison (1895) <i>Amphiuma</i>	Emerson (1905) <i>Typhlomolge</i>
Opercularis	Opercularis	d	Levator scapulae
Cucullaris	Cucullaris	d	Trapezius
Pectoralis	Pectoralis	Pectoralis major	Pectoralis
Supracoracoideus	Supracoracoideus	Supracoracoideus	Supra-coracoideus
Procoracohumeralis	Procoraco-humeralis	Coraco-humeralis	Pro-coraco-humeralis
Coracobrachialis longus	Coraco-brachialis longus	d	Coraco-brachialis longus
Anconaeus coracoideus	Anconaeus coracoideus	Triceps?	Anconaeus coracoideus
Anconaeus scapularis medialis	Anconaeus scapularis medialis	Triceps?	Anconaeus scapularis medius
Anconaeus humeralis lateralis	Anconaeus humeralis lateralis	Triceps?	Anconaeus humeralis lateralis
Anconaeus humeralis medialis	Anconaeus humeralis medialis	Triceps?	c
Latissimus dorsi	Dorso-humeralis	Latissimus dorsi	Latissimus dorsi
Dorsalis scapulae	Dorsalis scapulae	d	Supra-scapularis
Humeroantibrachialis	Humero-antibrachialis	Part of Deltoideus	Humero-antibrachialis inferior
Flexor digitorum communis	Flexor primordialis communis	Flexor digitorum communis	d
Flexor antebrachii et carpi radialis	Flexor antibrachii et carpi radialis	Flexor carpi radialis	d
Flexor antebrachii et carpi ulnaris	Flexor antibrachii et carpi ulnaris	d	d
Extensor digitorum communis	Extensor digitorum communis	d	d
Extensor antebrachii et carpi radialis	Extensor antibrachii et carpi radialis	d	d
Extensor antebrachii et carpi ulnaris	Extensor antibrachii et carpi ulnaris	d	d
Contraheentium caput longum	Caput longum musculorum contraheentium	d	d
Flexor accessorius lateralis	Flexor accessorius lateralis	d	d
Flexor accessorius medialis	Flexor accessorius medialis	d	d
Pronator profundus	Pronator profundus	d	d
Flexores breves superficiales	Flexores breves superficiales	d	d
Intermetacarpales	Intermetacarpales	d	d
Extensores digitorum breves	Extensores breves digitorum	d	d
Abductor et extensor digiti I	Abductor et extensor digiti I	d	d
Extensor lateralis digiti IV	Extensor lateralis digiti IV	d	d
Contraheentes digitorum	Contraheentes digitorum	d	d
Flexores breves profundi	Flexores breves profundi	d	d

^aNames in the first column are those used in this study.

^bBaird (1951) uses the same names as Francis (1934) for the muscles he describes: O, C, P, SC, PCH, CBL, LD and DS. A separate column is therefore omitted.

^cIndicates the muscle is missing.

^dIndicates the author does not describe the muscle.

A second intriguing finding was the incomplete separation of the ischioflexorius (ISF; Figs. 2 and 3) muscle from the puboischiotibialis (PIT; Fig. 2). Only the distal section of the ISF is easily distinguished from the neighboring fibers of the PIT. Of the other salamander species previously described, *Pseudoeurycea* (Baird, 1951), *Bolitoglossa* (Restrepo and Hoyos, 1998), *Paramesotriton* (Darevsky and Salomatina, 1989), and *Onychodactylus* (mentioned in Ashley-Ross, 1992) seem to share this characteristic. Unfortunately, the presence or absence of a distinct proximal portion of the ISF

does not correlate simply with our current understanding of salamander phylogeny (Gao and Shubin, 2001), but rather is a trait that must have arisen (or been lost) multiple times. Functionally, a two-part ISF may not make a great deal of difference to the typical demands of walking; Ashley-Ross (1995) showed that for *Dicamptodon* (which does have a distinct proximal ISF), the periods of muscle activity during the stride for the proximal PIT and the proximal ISF overlap almost completely. Thus, contraction of the proximal PIT may play the same role for stabilizing the distal ISF that a

TABLE 1. Synonymy of salamander forelimb muscles described for various genera (continued)

Gilbert (1973) <i>Necturus</i>	Mivart (1869) <i>Menopoma</i>	Restrepo & Hoyos (1998) <i>Bolitoglossa</i>	Smith (1927) <i>Triturus</i>
d	Levator anguli scapulae	Opercularis	Levator scapulae
Cucullaris	Trapezius	Cucullaris major and minor	Cucullaris
Pectoralis	Pectoralis	Pectoralis	Pectoralis
Supracoracoideus	Part of Coraco-brachialis	Supracoracoideus	Supracoracoideus
Procoracohumeralis	Subclavius	Procoracohumeralis	Procoracohumeralis
Coracobrachialis	Part of Coraco-brachialis,	Coracobrachialis longus	Coraco-brachialis longus
Anconaeus	Part of Biceps	Anconaeus coracoideus	d
Anconaeus	Triceps	Anconaeus scapularis	Anconaeus (Triceps) scapularis
Anconaeus	Triceps	Anconaeus humeralis	Anconaeus (Triceps) humeralis
Anconaeus	Triceps	Anconaeus humeralis medialis	Anconaeus (Triceps) humeralis medialis
Latissimus dorsi	Latissimus dorsi	Dorsohumeralis	Latissimus dorsi
Dorsalis scapulae	Deltoid	Dorsalis scapulae	Dorsalis scapulae
Humeroantebrachialis	Part of Biceps	Humero antibrachialis	Biceps brachii
Flexor primordialis communis	Flexor longus	Flexor primordialis communis	Flexor digiti communis
Flexor antebrachii et carpi radialis	Pronator teres	Flexor antibrachii et carpi radialis	Flexor carpi radialis
Flexor antebrachii et carpi ulnaris	d	Flexor antibrachii et carpi ulnaris	Flexor carpi ulnaris
Extensor digitorum communis	Extensor longus	Extensor digitorum communis	Extensor digiti communis
Extensor antebrachii et carpi radialis	Supinator longus	Extensor antibrachii et carpi radialis	Extensor carpi radialis
Extensor antebrachii et carpi ulnaris	Ulnaris	Extensor antibrachii et carpi ulnaris	Extensor carpi ulnaris
d	Flexor brevis	Caput longum musculorum contrahentium	d
d	d	Flexor accessories lateralis	d
d	d	Flexor accessorius medialis	d
d	d	Pronator profundus	d
d	d	Flexores breves superficiales	d
d	d	Intermetacarpales	d
d	d	Extensores digitorum breves	d
d	Extensor brevis	Abductor et extensor digiti I	d
d	d	Extensor lateralis digiti IV	d
d	d	d	d
d	d	d	d

proximal ISF would during walking. A question still to be resolved, then, is why have a separate proximal ISF in some taxa? Does the trait correlate with some other behavior, e.g., burrowing? Recordings of muscle activity patterns during activities other than walking would need to be obtained to address this issue.

An observation that may be related to the morphology of the ISF is the relatively large size of the femorofibularis (FMFB; Fig. 4) in *T. torosa*. Ashley-Ross (1992) found that there appeared to be a trade-off between the two muscles

in size: *Dicamptodon* and newly metamorphosed *Ambystoma* both possess a large ISF coupled with an extremely thin and narrow FMFB. In contrast, specimens of *Ambystoma* that were well past metamorphosis had a relatively narrow ISF and a robust FMFB. Likewise, Restrepo and Hoyos (1998) describe the FMFB of *Bolitoglossa* as being substantial, with an extensive insertion along much of the length of the fibula. Finally, Darevsky and Salomatina (1989) note the same trade-off in size between the ISF and FMFB in *Paramesotriton*. Francis (1934) has noted that

branches of the same nerve innervate the distal ISF and the FMFB; it is possible that the two muscles represent alternative solutions to the same functional demands of locomotion.

The forelimb musculature does not show as much regular variation as the hindlimb musculature across species. Complicating comparisons is the fact that few studies have examined the muscles of the forearm and manus (exceptions are Francis, 1934; Restrepo and Hoyos, 1998). However, among the muscles of the shoulder and upper arm, most variation seems to be in the relative size, not position, of various muscles. For example, the procoracohumeralis (PCH; Figs. 5 and 6) varies in size from large and robust in *Cryptobranchus* (Mivart, 1869), *Pseudoeurycea* (Baird, 1951), and *Bolitoglossa* (Restrepo and Hoyos, 1998) through average size (*Taricha*) to extremely thin and narrow in *Typhlomolge* (Emerson, 1905). A second example of variation in muscle size is the latissimus dorsi (LD; Fig. 6), which is large in *Typhlomolge* (Emerson, 1905), *Pseudoeurycea* (Baird, 1951), *Bolitoglossa* (Restrepo and Hoyos, 1998), and *Taricha*; the LD has a much less extensive origin in *Cryptobranchus* (Mivart, 1869).

Within an individual salamander, it is immediately apparent that the muscles of the forelimbs and hindlimbs share much of the same pattern, particularly in the distal limb segments (compare Figs. 2 and 5, 3 and 6). Indeed, the forearm and crus, as well as the manus and pes, show nearly identical muscular morphology. Furthermore, dorsal and ventral musculature (especially in the forearm) are essentially mirror images. The digits are controlled superficially by muscles originating from the distal end of the proximal limb segment; these muscles (EDCs in both limbs, FPC in the hindlimb, and FDC in the forelimb) all end in aponeuroses from which extend long tendons to the distal phalanges. Below this superficial layer are muscles that control torsional movements of the manus/pes (e.g., FAM, FAL, and PP) and of the crus and antebrachium itself (ECT, ETT, ECTF, EACR, EACU, FACR, and FACU). In the hindlimb, there is more differentiation between ventral and dorsal musculature; in the forelimb, ventral and dorsal sides appear nearly identical. Finally, the series of muscles that span from the plantar/palmar aponeurosis to the phalanges show indistinguishable arrangements between fore- and hindlimbs. The mirror-like arrangement of the muscles of the dorsal and ventral antebrachium would seem to argue that this limb segment has undergone little, if any, anatomical rearrangement due to selective pressure on locomotor demands. The hindlimb, in contrast, is thought to provide most of the power for locomotion (Barclay, 1946; Daan and Belterman, 1968; Edwards, 1977; Peters and Goslow, 1983) and therefore has altered its structures to make walking more efficient or powerful. While the salamander forelimb is known to have undergone evolutionary reduction in digit number (loss of digit V) (Shubin, 2002), correspondence in the morphology of its flexor and extensor muscles suggests that it may nonetheless retain the primitive pattern of musculature of the tetrapod limb, which may be of use in fossil reconstructions.

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