

- lution 1772–1775. Genesis Publications, Guildford, England.
- WHITEHEAD, P. J. P. 1978. The Forster collection of zoological drawings in the British Museum (Natural History). Bull. Brit. Mus. (Nat. Hist.), Hist. Ser. 6: 25–47.
- . 1986. The synonymy of *Albula vulpes* (Linnaeus, 1758) (Teleostei, Albulidae). *Cybio* 10:211–230.
- ZAMA, A. 1978. A grouper *Epinephelus albopunctulatus*, a synonym of *E. spiniger*, distinct from *E. truncatus*. *Japan. J. Ichthy.* 25:219–222.
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Ontogenetic Scaling of Hindlimb Muscles across Metamorphosis in the Tiger Salamander, *Ambystoma tigrinum*

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Metamorphosis in tiger salamanders involves a shift from aquatic to terrestrial life and consequently a shift in the gravitational load placed on locomotor muscles. Metamorphic mass changes in hindlimb muscles were examined in 12 larval and eight transformed *Ambystoma tigrinum* collected immediately before and after metamorphosis, respectively. Analyses of covariance revealed no significant differences in muscle masses of 16 hindlimb muscles from larvae and transformed individuals. Principal component analysis revealed that each muscle mass loaded high and positively on the first principal component, which we interpret to be a general vector correlated with the overall size of the animal. Principal components two and three failed to separate larvae and adults into discrete groups. Thus, unlike many jaw muscles, when corrected for body size, hindlimb muscles do not change in mass at metamorphosis, and the growth trajectory of the muscles established in the larva is extended with little or no change into early terrestrial life.

THE transition from water to land common during amphibian metamorphosis represents a system in which an individual organism radically changes its physiology and morphology in a short time span to function adequately in its new environment (Wilder, 1925; Dodd and Dodd, 1976; Duellman and Trueb, 1986). An example of a biomechanical complex that fulfills different tasks across metamorphosis is the locomotor system of the tiger salamander, *Ambystoma tigrinum*, which shifts from using lateral undulations of the body and tail as a primary means of movement in the water to quadrupedal locomotion using the limbs for

propulsion on land (Duellman and Trueb, 1986).

Several authors (e.g., Wilder, 1925; Etkin, 1964; Duellman and Trueb, 1986) have stated, on the basis of casual observation, that the limbs of urodeles undergo no significant metamorphosis, but, instead, follow a continuous growth trajectory established in the larva. However, the functional demands a terrestrial environment places on the limbs would appear to be very different from those an aquatic environment imposes, resulting from the loss of passive buoyant support. On land, at the very least, the limbs must be able to support the weight of the body, as well as provide forward propulsion, and sev-

eral authors have suggested that postmetamorphic salamanders should possess more robust limbs. Wilder (1925) found that metamorphosed salamanders are considerably more muscular than their larval forms, and Duellman and Trueb (1986) stated that the main power for propelling the body in adult salamanders comes from the hindlimbs. In addition, Latimer and Roofe (1964) have reported that the relative hindlimb length of just-metamorphosed tiger salamanders is significantly greater than that of larvae just prior to metamorphosis. Worthington and Wake (1971) stated that the pelvic girdle in larvae of *Ambystoma* becomes robust just before metamorphosis. Darevsky and Salomatina (1989) have shown changes in hindlimb myology associated with the move to terrestrial habits in *Paramesotriton deloustali*. Lauder and Reilly (1990) demonstrated a size increase in the muscle responsible for protracting the tongue in *A. tigrinum* and attributed this change to the metamorphic shift from aquatic suction feeding to terrestrial feeding by tongue projection. Metamorphic change has also been documented in anuran jaw adductor muscles, where larval muscle fiber populations degenerate during and after metamorphosis, being completely replaced by adult fiber populations (Alley, 1989); the adult muscles contain over 10 times as many fibers as the larval muscles. Sperry (1981) has shown that post-metamorphic growth of anuran hindlimb muscles is attributable to an increase in fiber number as well as an increase in individual fiber size. These observations suggest the a priori hypothesis that one should see an increase in the size of salamander hindlimb muscles as a consequence of metamorphosis itself in preparation for the move from an aquatic to a terrestrial environment. At present there are no quantitative data on either the locomotor biomechanics or limb morphology in metamorphosing salamanders.

Possible scaling patterns.—Figure 1 shows three hypothetical ways by which the mass of limb muscles might change at metamorphosis. The simplest is by extension of larval scaling, whereby the muscle mass increases in concert with overall body size (an index of which is given by snout-vent length); the growth trajectory remains the same throughout larval development and adulthood (Fig. 1A and B, larval scaling).

Alternatively, the relationship of muscle mass to body size may be altered at metamorphosis

in either of two ways. First, the growth trajectory of the muscle may change (Fig. 1A), increasing its rate of growth relative to body size (positive allometry) or decreasing its relative rate of growth (negative allometry). Second, a radical increase or decrease in muscle mass may be compressed into the relatively short time span of metamorphosis, and thereafter the muscle may revert to the same growth trajectory expressed in the larva for muscle mass relative to body size (Fig. 1B). This would result in a retention of larval scaling, with either a positive or negative transposition at metamorphosis. Lauder and Reilly (1990) observed the latter pattern in their study of metamorphic change in the jaw muscles of *A. tigrinum*, which showed all three of the patterns depicted in Fig. 1B: some muscles decreased substantially in mass, others increased in mass, whereas others exhibited no change at metamorphosis. Salamander hindlimb muscle mass might also be altered by a combination of allometric change and transposition to suit terrestrial locomotion.

The main goal of this paper is to characterize change in mass of 16 hindlimb muscles across metamorphosis in the tiger salamander, *A. tigrinum*. We test the hypothesis that some (or all) of these muscles show an increase in mass (and therefore estimated force generating capacity) as a purely metamorphic effect. These results provide a basis for further investigations of hindlimb functional morphology across metamorphosis.

MATERIALS AND METHODS

Specimens.—To measure change in hindlimb muscle mass resulting from purely metamorphic effects, specimens of *A. tigrinum* preserved just before and just after metamorphosis were used. Twelve larvae and eight transformed individuals from the collections of the Museum of Natural History, University of Kansas, were examined. Specimens were collected in a single season from the same pond and formed an overlapping continuum over a restricted size range (SVL being used as a measure of overall body size). Both larval and transformed specimens were collected in the water. Larvae (SVL 73–88 mm) were preserved immediately, and transformed specimens (SVL 84–99 mm), preserved after being kept in small terraria for approximately five months, were completely metamorphosed (Reilly and Lauder, 1990). Limb muscles presumably had been influenced minimally

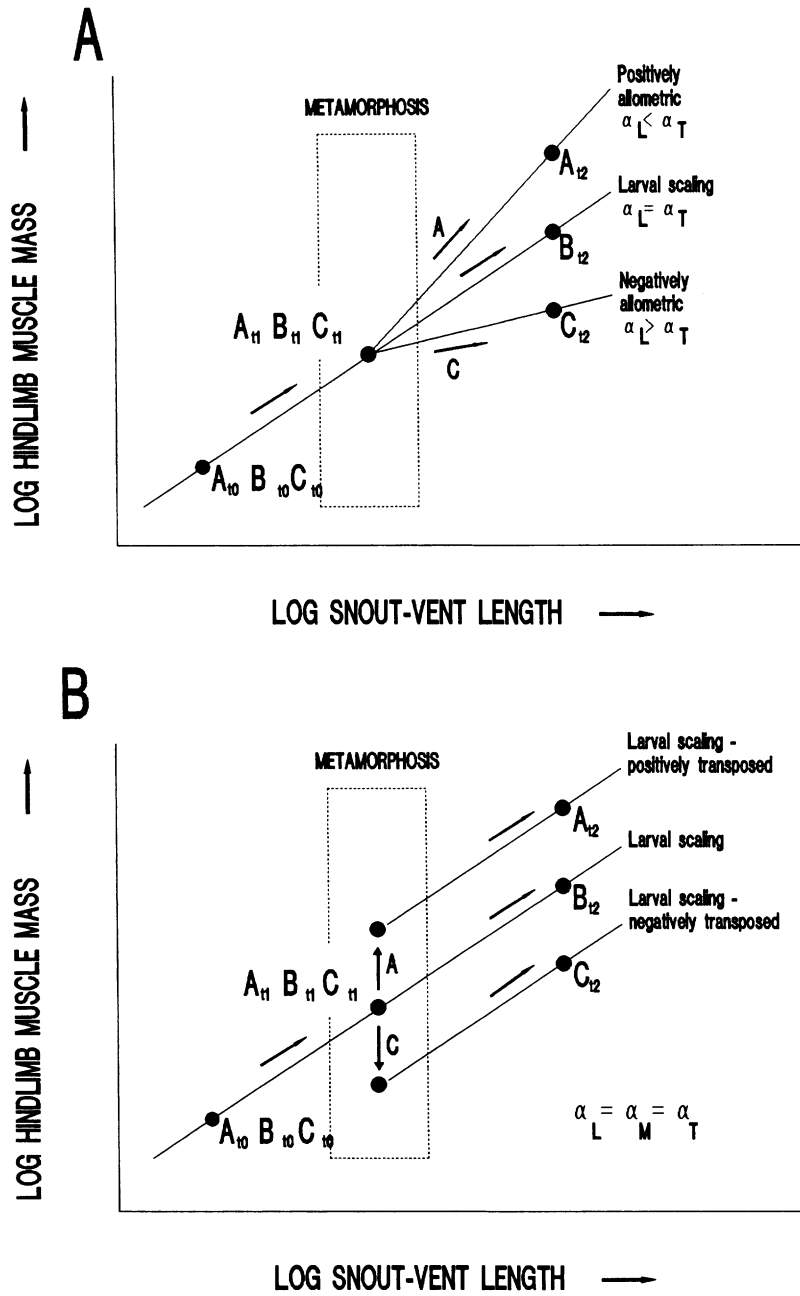


Fig. 1. Schematic diagram illustrating possible changes in ontogenetic trajectory of hindlimb muscle mass in a hypothetical metamorphosing animal. (A) Change in slope—at metamorphosis the growth rate of muscle mass changes, becoming either higher (positive allometry) or lower (negative allometry) than body size growth rate. Alpha represents the slope of the ontogenetic trajectory. (B) Transposition—at metamorphosis the larval growth rate is retained, but muscle mass undergoes a dramatic increase (positive transposition) or decrease (negative transposition) during the period of metamorphosis itself.

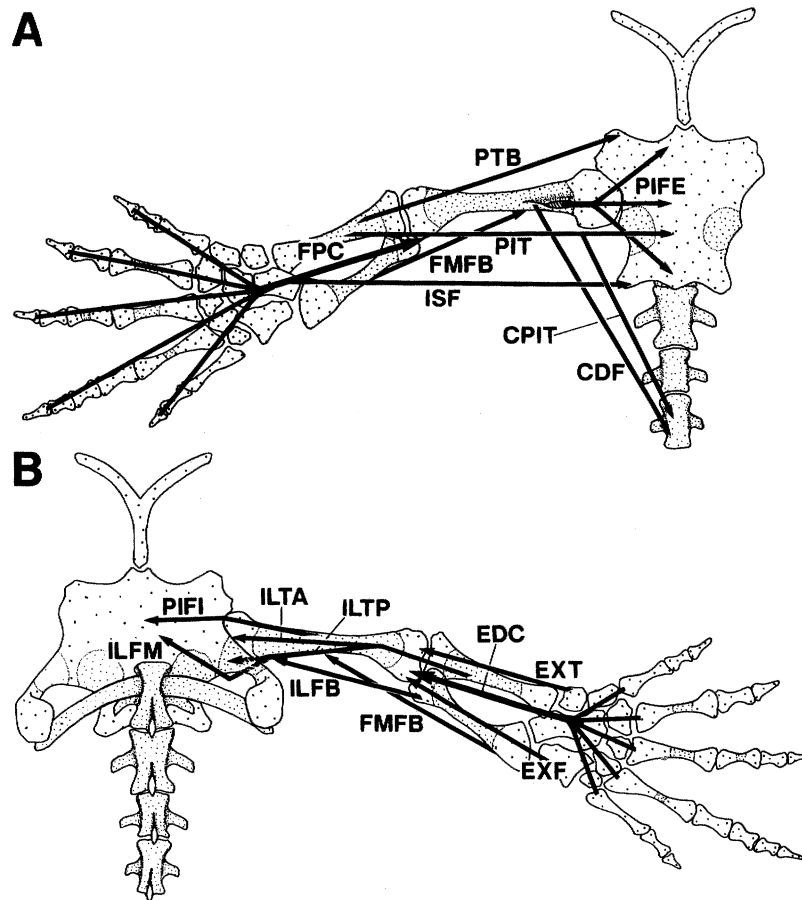


Fig. 2. Schematic diagram of the hindlimb of transformed *Ambystoma tigrinum*. Heavy black lines show the lines of action of the muscles studied. Arrowheads are on the points of origin. Fine stipple indicates bone; coarse stipple represents cartilage. (A) Ventral view. (B) Dorsal view. Abbreviations: CPIT = M. caudalipuboischiotibialis; CDF = M. caudofemoralis; PTB = M. pubotibialis; PIFE = M. puboischiofemoralis externus; PIT = M. puboischiotibialis; ISF = M. ischioflexorius; PIFI = M. puboischiofemoralis internus; ILFM = M. iliofemoralis; ILFB = M. iliofibularis; ILTA = M. iliotibialis anterior; ILTP = M. iliotibialis posterior; FMFB = M. femorofibularis; FPC = M. flexor primordialialis communis; EDC = M. extensor digitorum communis; EXF = M. extensor fibularis; EXT = M. extensor tibialis.

by training effects (muscle growth in response to active terrestrial locomotion). These same specimens were used in analyses of metamorphic change in the cranial musculature (Lauder and Reilly, 1990).

Measurements.—Sixteen muscles (Table 1) of the thigh and shank of each specimen were removed on both left and right sides of the body and weighed. All muscles were removed by flaying them from both origin and insertion with a pair of fine sharpened forceps, or by cutting origin/insertion tendons with fine scissors. Dis-

sections were performed with the aid of a Zeiss IVB dissecting microscope. The detailed morphology of these muscles will be described elsewhere (Ashley, unpubl.). Only a brief description of each muscle's origin and insertion is provided in the results, as well as of function (for the two muscles for which this is known). Muscle terminology follows that of Francis (1934), except where noted. For the purposes of this study, the pubifemoralis and ischiofemoralis muscles (not illustrated) were considered to be part of the puboischiofemoralis externus (PIFE) and were removed and weighed as a

TABLE 1. MEAN MUSCLE MASS (mg \pm SE) FOR 16 HINDLIMB MUSCLES AND SNOUT-VENT LENGTH (mm \pm SE) FOR LARVAL (n = 12) AND TRANSFORMED (n = 8) *Ambystoma tigrinum*.

Muscle	Muscle mass	
	Larvae	Transformed
Caudalipuboischiotibialis (CPIT)	7.3 \pm 0.5	17.4 \pm 2.7
Pubotibialis (PTB)	5.1 \pm 0.4	12.0 \pm 2.0
Puboischiotibialis (PIT)	34.2 \pm 3.4	83.6 \pm 13.5
Ischioflexorius (ISF)	6.1 \pm 0.7	13.9 \pm 1.8
Iliofibularis (ILFB)	2.2 \pm 0.2	5.5 \pm 1.1
Iliotibialis anterior (ILTA)	4.5 \pm 0.4	8.7 \pm 1.2
Iliotibialis posterior (ILTP)	4.1 \pm 0.4	8.6 \pm 1.1
Femorofibularis (FMFB)	1.3 \pm 0.1	3.0 \pm 0.4
Caudofemoralis (CDF)	14.2 \pm 1.1	37.4 \pm 6.2
Puboischiofemoralis externus (PIFE)	21.4 \pm 2.1	54.2 \pm 8.8
Puboischiofemoralis internus (PIFI)	24.7 \pm 2.4	53.4 \pm 8.1
Iliofemoralis (ILFM)	4.4 \pm 0.4	10.2 \pm 1.7
Flexor primordialis communis (FPC)	23.9 \pm 2.2	62.9 \pm 8.7
Extensor digitorum communis (EDC)	5.7 \pm 0.5	12.2 \pm 1.7
Extensor fibularis (EXF)	5.3 \pm 0.5	14.8 \pm 2.5
Extensor tibialis (EXT)	4.8 \pm 0.5	12.7 \pm 1.7
Snout-vent length (SVL)	78.8 \pm 1.5	91.1 \pm 1.9

complex with PIFE. Muscle positions are shown in Figure 2; names and abbreviations are also given in Table 1.

As the muscles were dissected, they were placed in covered tissue culture wells containing 70% EtOH. The mass of each muscle was determined to the nearest 0.0001 g on a Mettler analytical balance after gentle blotting. Because of the small size of the muscles, each was weighed three times, and the average of the three masses was recorded. These average muscle masses for both sides of the body were then themselves averaged to yield the value for muscle mass used in the statistical analyses.

Statistical analyses.—Because individuals varied in snout-vent length, we used analyses of covariance (ANCOVAs) to compare slopes and intercepts of regression lines for larvae and transformed specimens. \log_{10} muscle mass was regressed against \log_{10} SVL (used as a measure of body size). If the slopes of the regression lines were not significantly different, intercepts for the parallel regression lines were compared. ANCOVA was thus used to compare the pre- to postmetamorphic ontogenetic trajectories of larval and transformed individuals. Because multiple comparisons were being made, we used a conservative value of 0.01 as the significance level.

To examine multivariate effects of metamor-

phosis, we used multivariate analysis of covariance (MANCOVA), and conducted a principal component analysis (PCA) on eight representative muscle masses using \log_{10} -transformed data and the covariance matrix. The muscles chosen were a mix of dorsal (EDC, ILTA, PIFI) and ventral (CDF, FPC, ISF, PIT), flexor (CDF, FMFB, FPC, ISF, PIT) and extensor (EDC, ILTA, PIFI), thigh (CDF, ILTA, ISF, PIFI, PIT) and shank (EDC, FMFB, FPC), and large (CDF, FPC, PIFI, PIT) and small muscles (EDC, FMFB, ILTA).

RESULTS

Morphology.—Dissections revealed no discernible change over metamorphosis in muscle orientation or fiber angle. All muscles showed parallel-fibered architecture; no evidence of pinnate arrangement was noted in any larval or transformed muscle. We present here a brief description of the muscles used in our analyses.

Two muscles originate on the third postsacral vertebra (see Fig. 2B). The caudalipuboischiotibialis (CPIT; Fig. 2A) inserts by a short tendon onto the puboischiotibialis. The caudofemoralis (CDF; Fig. 2A; Gilbert, 1973) inserts on the posterior face of the femur. It acts to cause rotation about the long axis of the femur and aids in hip retraction (Peters and Goslow, 1983).

A total of six muscles arises from the pubo-

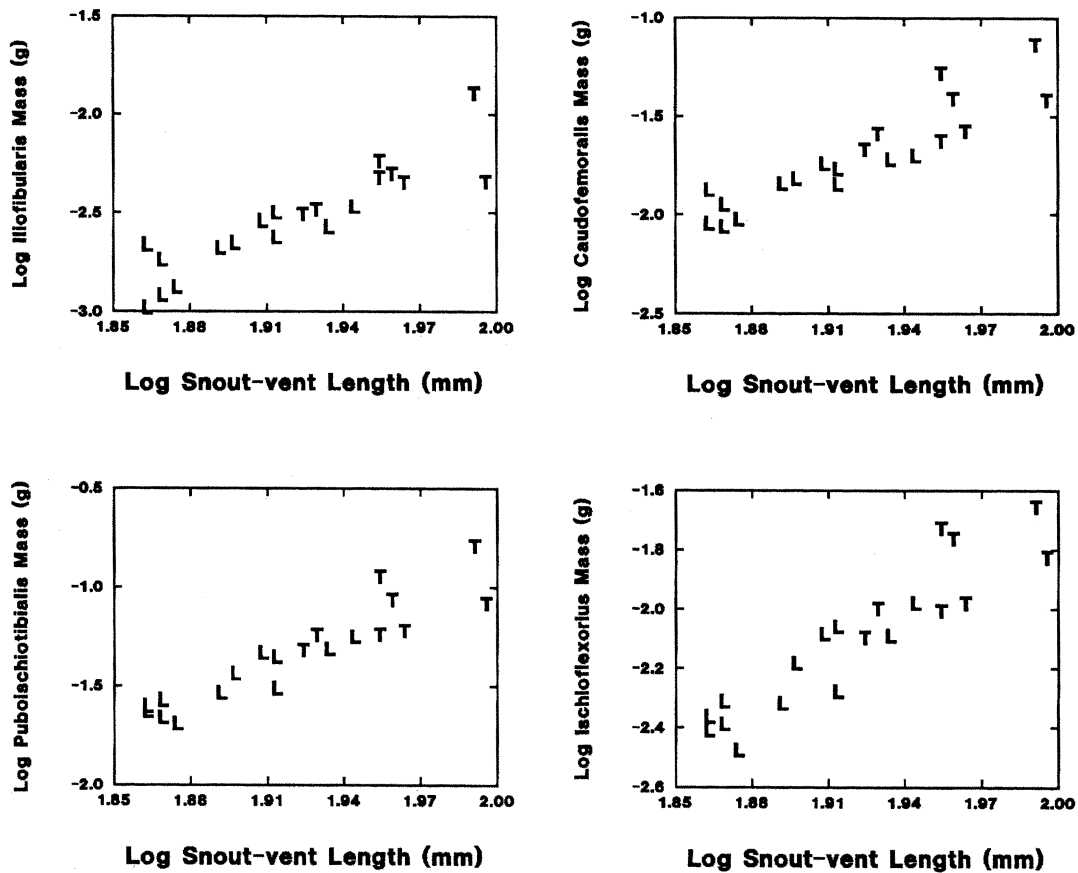


Fig. 3. Sample plots of \log_{10} muscle mass against \log_{10} snout-vent length for four representative muscles. Note that larval (L) and transformed (T) specimens share the same ontogenetic trajectory.

ischial plate. Four of these originate from its ventral face. The pubotibialis (PTB; Fig. 2A) is the most anterior of the ventral group, lying along the anterior border of the thigh. It spans two joints, inserting on the proximal tibia. The puboischiofemoralis externus (PIFE; Fig. 2A) is a deep, fan-shaped (though not pinnate) muscle inserting on the ventral femur.

The puboischiotibialis (PIT; Fig. 2A) crosses two joints. It is the largest of the hindlimb muscles, inserting on the tibia. The PIT functions in knee flexion, hip stabilization, and hip retraction (Peters and Goslow, 1983). The ischioflexorius (ISF; Fig. 2A) is the most posterior of these four ventral muscles and is unique in that it is effectively a three-joint muscle, inserting on the plantar fascia covering the flexor primordialis communis.

The last two muscles originating from the pubo-ischiac plate arise from its dorsal surface (facing the interior of the abdomen). The pu-

boischiofemoralis internus (PIFI; Fig. 2B) inserts on the anterior face of the femur. The iliofemoralis (ILFM; Fig. 2B) originates posterior and lateral to the PIFI. It curves around the posterior border of the ilium to insert on the posterior surface of the femur.

Three muscles crossing the dorsal aspect of the thigh originate on the ilium. The iliotibialis anterior (ILTA; Fig. 2B) and iliotibialis posterior (ILTP; Fig. 2B) are two-joint muscles that insert via a common tendon onto the proximal tibia. The ILTA arises from the anterior border of the ilium, whereas the ILTP arises from the lateral face of the ilium via a tendon of origin that it shares with the iliofibularis (ILFB; Fig. 2B). The ILFB inserts onto the proximal fibula.

Five muscles take their origin from the femur. The femorofibularis (FMFB; Fig. 2) is a deep muscle arising from the posterior face of the femur and inserting on the posterior face

TABLE 2. PARAMETERS FOR LINEAR REGRESSIONS OF \log_{10} MUSCLE MASS (g) ON \log_{10} SNOUT-VENT LENGTH (mm) FOR LARVAL ($n = 12$) AND TRANSFORMED ($n = 8$) *Ambystoma tigrinum*. ANCOVA indicates significance of tests for transmetamorphic variation in larvae vs. transformed salamanders. The 0.01 level was used to evaluate ANCOVA test significance.

Muscle	Larvae			Transformed			ANCOVA <i>P</i> value		
	Slope	Intercept	<i>P</i> value	Slope	Intercept	<i>P</i> value	Slope	Intercept	<i>R</i> ²
Caudalipuboischiotibialis	2.939	-7.718	0.006	5.206	-11.990	0.039	n.s.	n.s.	0.827
Pubotibialis	4.074	-10.032	0.000	6.013	-13.739	0.017	n.s.	n.s.	0.859
Puboischiotibialis	4.821	-10.628	0.000	4.807	-10.529	0.060	n.s.	n.s.	0.861
Ischioflexorius	5.044	-11.805	0.000	4.325	-10.354	0.057	n.s.	n.s.	0.858
Iliofibularis	4.797	-11.775	0.001	5.266	-12.620	0.050	n.s.	n.s.	0.818
Iliotibialis anterior	3.981	-9.907	0.001	4.359	-10.624	0.035	n.s.	n.s.	0.825
Iliotibialis posterior	4.502	-10.947	0.000	3.585	-9.107	0.063	n.s.	n.s.	0.849
Femorofibularis	4.629	-11.698	0.004	5.361	-13.053	0.018	n.s.	n.s.	0.823
Caudofemoralis	3.956	-9.362	0.000	4.944	-11.149	0.064	n.s.	n.s.	0.854
Puboischiofemoralis externus	4.726	-10.651	0.000	5.901	-12.865	0.023	n.s.	n.s.	0.860
Puboischiofemoralis internus	4.451	-10.067	0.000	5.745	-12.557	0.007	n.s.	n.s.	0.877
Iliofemoralis	4.132	-10.207	0.002	6.413	-14.596	0.012	n.s.	n.s.	0.842
Flexor primordialis communis	4.174	-9.553	0.001	5.861	-12.714	0.013	n.s.	n.s.	0.886
Extensor digitorum communis	4.312	-10.440	0.000	5.781	-13.266	0.006	n.s.	n.s.	0.893
Extensor fibularis	4.635	-11.089	0.001	5.305	-12.258	0.023	n.s.	n.s.	0.867
Extensor tibialis	4.507	-10.879	0.000	4.915	-11.549	0.020	n.s.	n.s.	0.901

of the fibula. The flexor primordialis communis (FPC; Fig. 2A), a ventral muscle, is the largest muscle of the shank, taking its origin from the distal end of the femur and inserting onto the plantar fascia, which extends along the digits via tendons attached to the distal phalanges.

Three muscles arise from the distal dorsal surface of the femur. The extensor digitorum communis (EDC; Fig. 2B) is a fan shaped muscle inserting onto the proximal ends of the metatarsals. The extensor fibularis (EXF; Fig. 2B; Gilbert, 1973) inserts onto both the fibula (this insertion not illustrated) and the fibulare. The extensor tibialis (EXT; Fig. 2B; Gilbert, 1973) effectively mirrors the EXF, inserting partially onto the tibia (not illustrated) and partially onto the tibiale and prehallux.

Statistics.—Body size (as indicated by snout-vent length) was larger for transformed individuals (SVL 84–99 mm) than for larvae (SVL 73–88 mm). Summary statistics for larval and transformed individual muscle masses are presented in Table 1. For all muscles, the mean muscle masses (not size corrected) are greater for the transformed individuals than for the larvae. Representative plots of \log_{10} muscle mass vs \log_{10} snout-vent length for four muscles are shown in Figure 3.

Individual muscle regression parameters and

ANCOVA tests for larval and transformed samples are given in Table 2. Analysis of covariance indicates that, for all muscles measured, neither the slope nor the intercept of the regression lines through larval and transformed muscles was significantly different between the two groups (Table 2). MANCOVA showed neither significant differences between larval and transformed groups (Wilks' lambda = 0.042_(16,2), $P = 0.293$) nor a significant interaction term (Wilks' lambda = 0.04_(16,1), $P = 0.574$).

Principal component analysis of muscle masses for eight representative muscles (Fig. 4) demonstrates a strong overall size effect. Larvae and transformed individuals form separable groups on PC1 (Fig. 4A), and all variables load high and positively on PC1 (Fig. 4C), suggesting that PC1 is a general size vector (Bookstein et al., 1985). Larval and transformed individuals do not separate along PC2 or PC3 (Fig. 4B), and loadings on these axes are uniformly low (Fig. 4D) with no discernible pattern.

DISCUSSION

When corrected for animal size, no hindlimb muscle masses increase across metamorphosis (Table 2). In salamanders living in the wild, it is possible that limb muscle masses undergo a

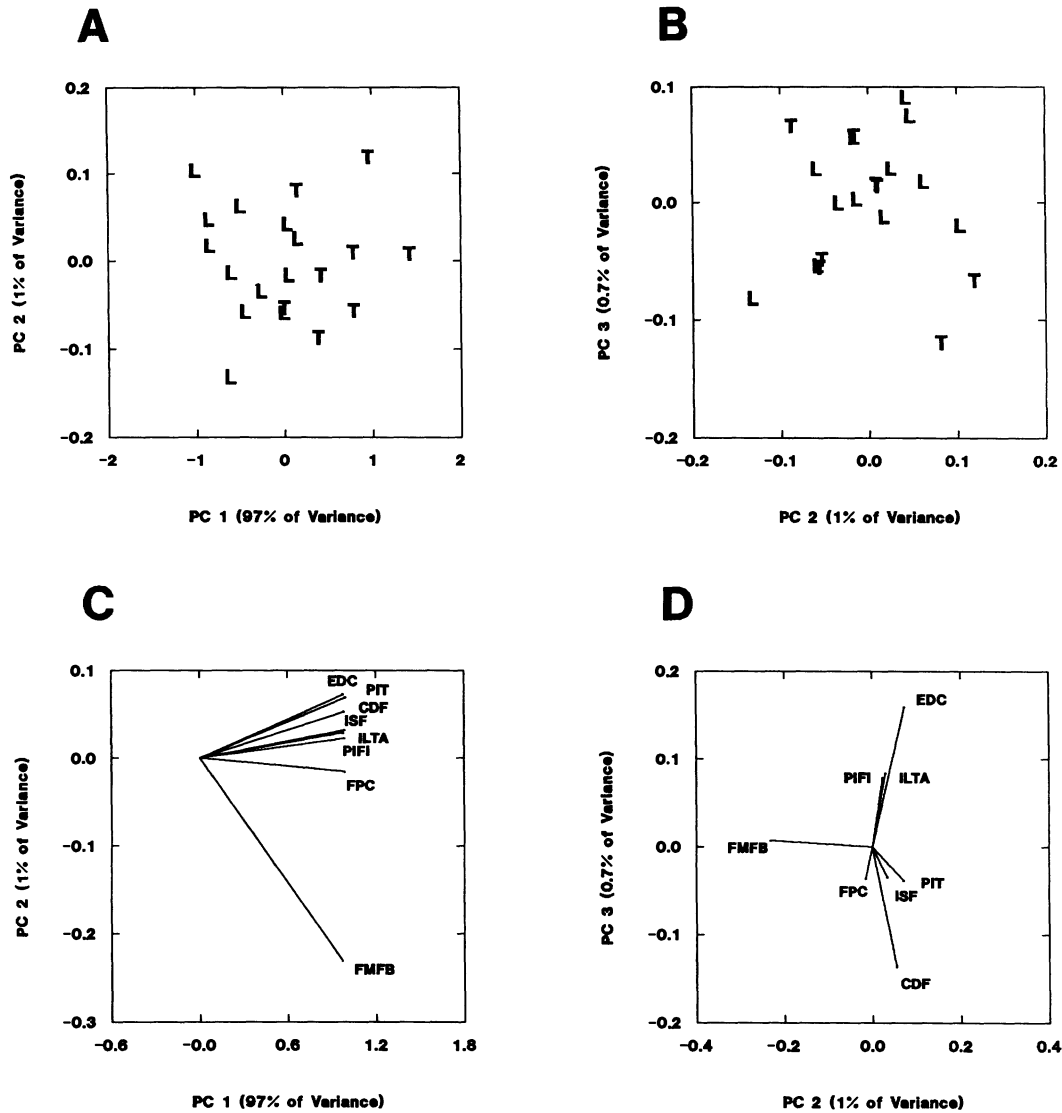


Fig. 4. Principal component analysis of masses of eight representative muscles of the hindlimb of *Ambystoma tigrinum*. (A, B) Scatters of larval and transformed individuals on the first three principal components of muscle masses. Note that metamorphic stages separate on PC space purely on the basis of overall size (PC1). (C, D) Correlations of muscle mass with corresponding principal components.

positive transposition (Fig. 1B) or positive allometric change in growth rate (Fig. 1A) when transformed individuals leave the water and subject the muscles to chronic load-bearing in terrestrial locomotion. Worthington and Wake's (1971) observation that the pelvic girdle in *Ambystoma* becomes well developed only when the larva nears metamorphosis suggests that anti-gravity muscles such as the puboischiotibialis

(PIT) and the puboischiofemoralis externus (PIFE), both of which originate on the pelvic girdle, would show the largest increase in mass in response to terrestrial load bearing. Because our transformed specimens were kept in restricted terraria, we were unable to test this hypothesis.

Powers (1907) described, at least qualitatively, just such a correlation between the robust-

ness of the hindlimbs and their degree of use or disuse. Larval *A. tigrinum* that were forced to adopt a posture in their aquaria in which the limbs had to support the body weight developed very robust hindlimbs. In contrast, larvae that were kept in deep water-filled jars showed no such hypertrophy of the hindlimbs, and wild-caught adults that were kept in such jars showed a "noticeable degeneration" of the hindlimbs (Powers, 1907, p. 243). Powers (1907) concluded, however, that relative robustness of many body features, including the hindlimbs, was primarily dependent upon the nutrition of the animal and that the resulting variability, particularly in the larvae, was great enough to obscure many growth trends and metamorphic changes.

In light of Alley's (1989) findings on the turnover of muscle fiber populations across metamorphosis in anuran jaw muscles, it is surprising to us that no radical increase in hindlimb muscle mass was found in the tiger salamander. Lauder and Reilly (1990) demonstrated that metamorphosis of the cranial musculature of tiger salamanders involves a significant *negative* transposition of the growth trajectories of two muscles, the rectus cervicis and depressor mandibulae, a *positive* transposition of the growth trajectory of the subarcualis rectus 1, and no change in the trajectories of the other muscles studied. Our present results on the hindlimb muscles of the same specimens indicate that different mechanisms operate to prepare the feeding and locomotor systems for terrestrial life. This conclusion is based on the knowledge that the skull and hyobranchial apparatus undergo considerable transformation in the switch from aquatic suction feeding to terrestrial feeding by tongue projection (Reilly and Lauder, 1990). In contrast, the hindlimbs are functional in both the larvae (Coghill, 1929; Faber, 1956), which paddle about and walk on the bottom of ponds, and in transformed terrestrial individuals. However, the aquatic and terrestrial environments have been noted to impose different requirements on the walking apparatus of urodeles. Faber (1956) states that the movements of both fore- and hindlimbs in walking underwater are distinctly different from their movements in terrestrial locomotion in *Triturus taeniatus*. In their anatomical study of the hindlimbs of *Parame-sotriton deloustali*, Darevsky and Salomatina (1989) attributed the major differences in myology and osteology to the animal's aquatic or terrestrial habits. Terrestrial adults were characterized by greatly hypertrophied femorofibu-

laris (FMFB) muscles, which inserted onto a pronounced crista on the fibula, whereas adults captured in water possessed unusually large ischioflexorius (ISF) muscles. Neither larvae nor aquatic adults possessed the fibular crista (Darevsky and Salomatina, 1989).

The maintenance of the larval growth trajectory of hindlimb muscle mass in our transformed specimens (whose movements were restricted by the small terraria in which they were kept), when compared to the changes observed by other workers in wild-caught individuals, suggests that the limbs of metamorphosed salamanders may retain a plasticity that enables them to remodel themselves to suit either a terrestrial or aquatic existence. The particular morphology of adult salamander limbs would in this way be dictated by the functional requirements placed upon them (i.e., gravitational load on land) rather than fixed metamorphic anatomical reorganization. Analysis of hindlimb muscle mass from wild-caught, fully terrestrial adult tiger salamanders as well as neotenes is needed to test this hypothesis.

MATERIAL EXAMINED

Institutional abbreviation follows that of Leviton et al. (1985). Twelve *Ambystoma tigrinum* larvae (KU 89119–89122, 89124, 89128, 89135, 89140, 89141, 89144, 89145, 89149) and eight transformed individuals (KU 89091, 89096, 89102, 89107–89111). All specimens collected from ponds in Colorado Springs, Colorado.

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LITERATURE CITED

- ALLEY, K. E. 1989. Myofiber turnover is used to retrofit frog jaw muscles during metamorphosis. *Am. J. Anat.* 184:1–12.
 BOOKSTEIN, F., B. CHERNOFF, R. ELDER, J. HUMPHRIES, G. SMITH, AND R. STRAUSS. 1985. Morphometrics in evolutionary biology. Academy of Natural Sciences, Philadelphia, Pennsylvania.
 COGHILL, G. E. 1929. Anatomy and the problem of

- behavior. Hafner Publishing Co., New York, New York.
- DAREVSKY, I. S., AND N. I. SALOMATINA. 1989. Notes on hind limb structure in the salamander, *Paramesotriton deloustali*, and its mode of life. *J. Herpetol.* 23(4):429-433.
- DODD, M. H. I., AND J. M. DODD. 1976. The biology of metamorphosis, p. 467-599. *In: Physiology of the amphibia*. B. Lofts (ed.). Academic Press, New York, New York.
- DUELLMAN, W. E., AND L. TRUEB. 1986. *Biology of amphibians*. McGraw-Hill Book Co., New York, New York.
- ETKIN, W. 1964. Metamorphosis, p. 427-468. *In: Physiology of the amphibia*. J. A. Moore (ed.). Academic Press, New York, New York.
- FABER, J. 1956. The development and coordination of larval limb movements in *Triturus taeniatus* and *Ambystoma mexicanum* (with some notes on adult locomotion in *Triturus*). *Arch. Neerl. Zool.* 11:498-517.
- FRANCIS, E. T. B. 1934. *The anatomy of the salamander*. Oxford University Press, London, England.
- GILBERT, S. G. 1973. *Pictorial anatomy of the Neotriturus*. University of Washington Press, Seattle, Washington.
- LATIMER, H. B., AND P. G. ROOFE. 1964. Weights and linear measurements of the body and organs of the tiger salamander, before and after metamorphosis, compared with the adult. *Anat. Rec.* 148:139-147.
- LAUDER, G. V., AND S. M. REILLY. 1990. Metamorphosis of the feeding mechanism in tiger salamanders (*Ambystoma tigrinum*): the ontogeny of cranial muscle mass. *J. Zool. London* 222:59-74.
- LEVITON, A. E., R. H. GIBBS, JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985:802-832.
- PETERS, S. E., AND G. E. GOSLOW. 1983. From salamanders to mammals: continuity in musculoskeletal function during locomotion. *Brain Behav. Evol.* 22:191-197.
- POWERS, J. H. 1907. Morphological variation and its causes in *Ambystoma tigrinum*. *University Studies of University of Nebraska* 7:197-270.
- REILLY, S. M., AND G. V. LAUDER. 1990. Metamorphosis of cranial design in tiger salamanders (*Ambystoma tigrinum*): a morphometric analysis of ontogenetic change. *J. Morph.* 204:121-137.
- SPERRY, D. G. 1981. Fiber type composition and post-metamorphic growth of anuran hindlimb muscles. *Ibid.* 170:321-345.
- WILDER, I. W. 1925. *The morphology of amphibian metamorphosis*. Smith College, Northampton, Massachusetts.
- WORTHINGTON, R. D., AND D. B. WAKE. 1971. Larval morphology and ontogeny of the ambystomatid salamander, *Rhyacotriton olympicus*. *Am. Midl. Nat.* 85:349-365.

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