

Functional and Morphological Variety in Trunk Muscles of Urodela

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ABSTRACT. Trunk musculature in Urodela species varies by habitat. In this study, trunk musculature was examined in five species of adult salamanders representing three different habitats: aquatic species, *Amphiuma tridactylum* and *Necturus maculosus*; semi-aquatic species, *Cynops pyrrhogaster*; terrestrial species, *Hynobius nigrescens* and *Ambystoma tigrinum*. More terrestrial species have heavier dorsal and ventral trunk muscles than more aquatic forms. By contrast, the lateral hypaxial musculature was stronger in more aquatic species. The number of layers of lateral hypaxial musculature varied among Urodela species and did not clearly correlate with their habitats. The *M. rectus abdominis* was separated from the lateral hypaxial musculature in both terrestrial and semi-aquatic species. In aquatic species, *M. rectus abdominis* was not separated from lateral hypaxial musculature. Lateral hypaxial musculature differed in thickness among species and was relatively thinner in terrestrial species. In more terrestrial species, dorsal muscles may be used for stabilization and ventral flexing against gravity. Ventral muscle may be used in preventing dorsally concave curvature of the trunk by dorsal muscles and by weight. The lengthy trunk supported by limbs needs muscular forces along the ventral contour line in more terrestrial species. And, the locomotion on well-developed limbs seems to lead to a decrease of the lateral hypaxial musculature.

KEY WORDS: Caudata, locomotion, muscle, salamander, Urodela.

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Main habitats of adult salamanders differ according to species. Three categories of species have been studied in the past: fully aquatic species, semi-aquatic (both aquatic and terrestrial) species and fully terrestrial species [7, 15, 16]. During terrestrial walking and swimming, the trunks of salamanders move in an undulatory fashion [16]. During swimming, axial muscles do lateral undulations, while the limbs are pressed against the body [10]. During terrestrial walking, salamanders bend the body in standing waves, whereas the limbs act as anchors and contribute to stride length [2]. Body propulsion is conducted by concerted trunk and limb muscles [2, 10]. In these two patterns of lateral bending of trunk in swimming and walking, trunk musculature is activated sequentially or simultaneously [6, 9]. The activity of hypaxial muscles during walking and swimming has been recorded in *Dicamptodon ensatus* [4] and *Ambystoma tigrinum* [3]. However, few studies have quantified and observed trunk musculature in detail in Urodela species. Schilling and Deban [19] quantified muscle mass and fiber-type distribution of epaxial muscles in *Ambystoma*, and Azizi *et al.* [1]

quantified and observed the myosepta of *Siren lacertina* in detail. In these studies, morphological differences in trunk musculature of salamanders according to ecological habitat were not clarified. Although Simons and Brainerd [21] examined cross sections of trunk muscles for a quantitative comparison, no studies have been conducted to determine the weight of all trunk muscles. Quantification of *M. intertransversarius* and *M. interspinalis* by cross-section is difficult, because these muscles are nestled between vertebrae. In order to obtain quantitative data, we decided to take the weights of the muscles. Cross sectional area determines the force which can be produced by muscle, while the length of the muscle determines the distance through which it can be contracted. Then, it is implied that cross sectional area multiplied by muscle length is the work which can be performed by the muscle. Cross sectional area multiplied by length is equal to the volume of the muscle, and volume is proportional to weight. Therefore, we weighed muscles to get the product of its work.

The purpose of this paper was to characterize and quantify morphological variations in trunk musculature in salamanders of different ecotypes. Morphological variations in trunk musculature of salamanders were investigated in detail by weighing each trunk muscle. We expected differences in each trunk muscle ratio among species according to ecotype. A theory was also established regarding environmental adaptations for locomotion in aquatic or terrestrial environments.

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Table 1. Specimens used in this study

Species	Habitat	SVL* (mm)
<i>Amphiuma tridactylum</i>	Aquatic	408
		434
		471
<i>Necturus maculosus</i>	Aquatic	175
		172
		168
<i>Cynops pyrrhogaster</i>	Semi-aquatic	53
		48
		45
<i>Hynobius nigrescens</i>	Terrestrial	70
		72
		73
<i>Ambystoma tigrinum</i>	Terrestrial	111
		103
		86

*Snout-vent length.

MATERIALS AND METHODS

Specimens: Five species of adult salamanders representing five families were examined in this study (Table 1). Aquatic species included *Amphiuma tridactylum* (n=3) and *Necturus maculosus* (n=3), which have elongated bodies and shortened limbs (*A. tridactylum* more so than *N. maculosus*). Semi-aquatic species were represented by *Cynops pyrrhogaster* (n=3), which has a short body and relatively robust limbs. Terrestrial species included *Hynobius nigrescens* (n=3) and *Ambystoma tigrinum* (n=3), which have short trunks and robust limbs. These specimens were deposited at The University Museum, The University of Tokyo. Specimens were fixed in straight body position using 10% formalin and preserved in 70% ethanol solution.

Trunk musculature consists of the following muscles. *M. dorsalis trunci* makes up most of the epaxial muscle mass and *M. interspinalis*, *M. intertransversarius* and *M. subvertebralis* are perivertebral muscles. *M. obliquus externus*, *M. obliquus externus superficialis*, *M. obliquus externus profundus*, *M. obliquus internus* and *M. transversus abdominis* are

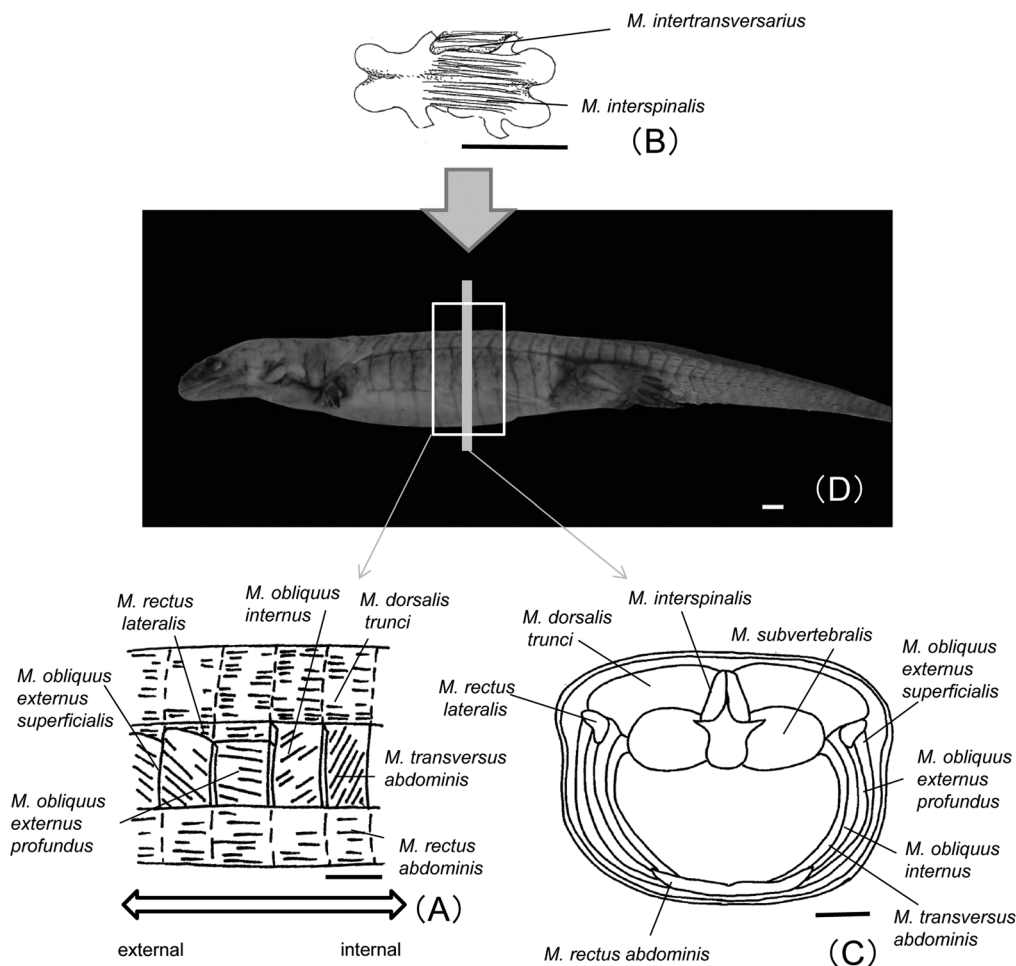


Fig. 1. *Ambystoma tigrinum* (A): Lateral view of trunk musculature (B): Dorsal view of trunk musculature after removal of *M. dorsalis trunci*. (C): Cross-sectional view. (D): Lateral view. Scale bar=5 mm.

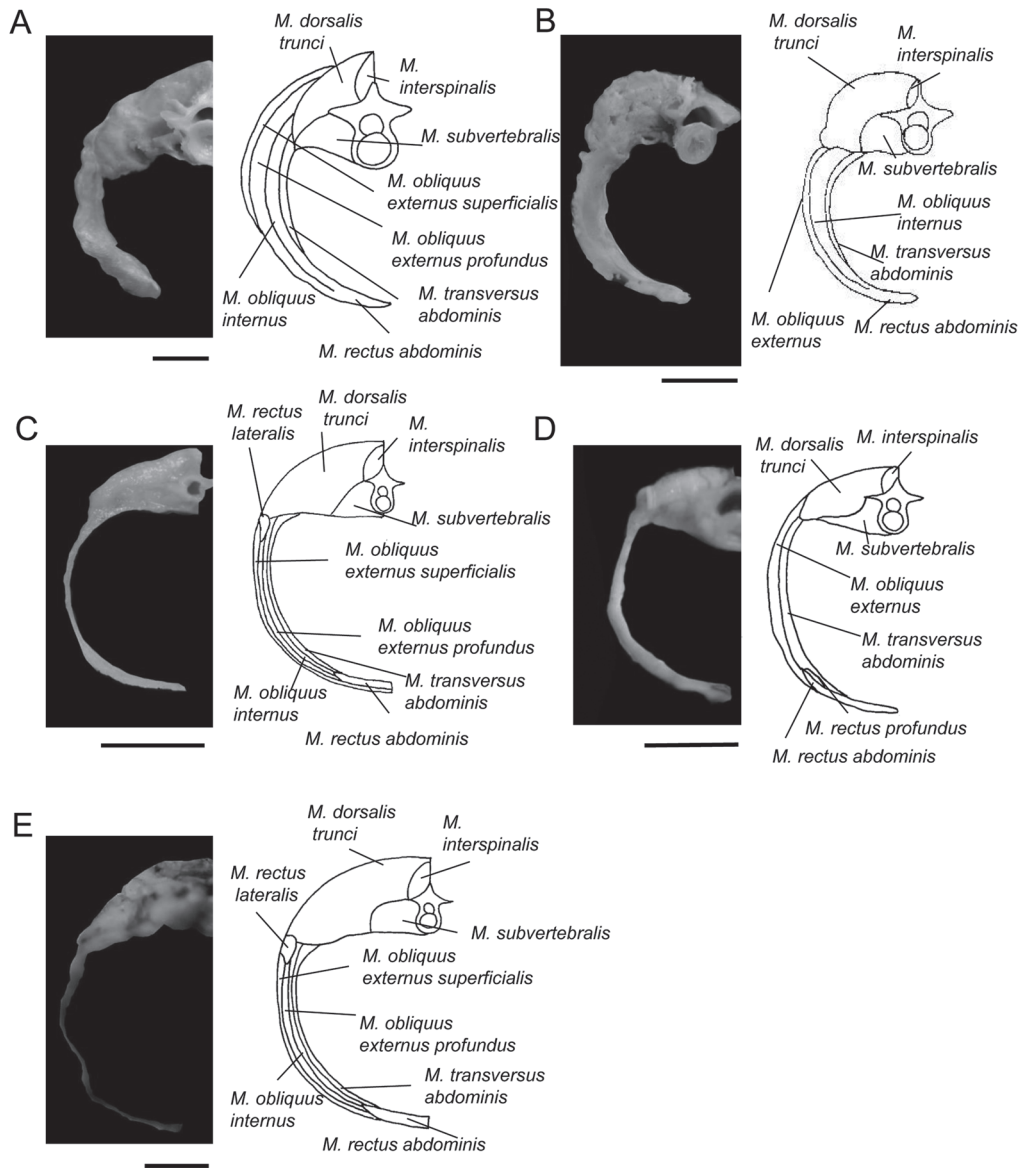


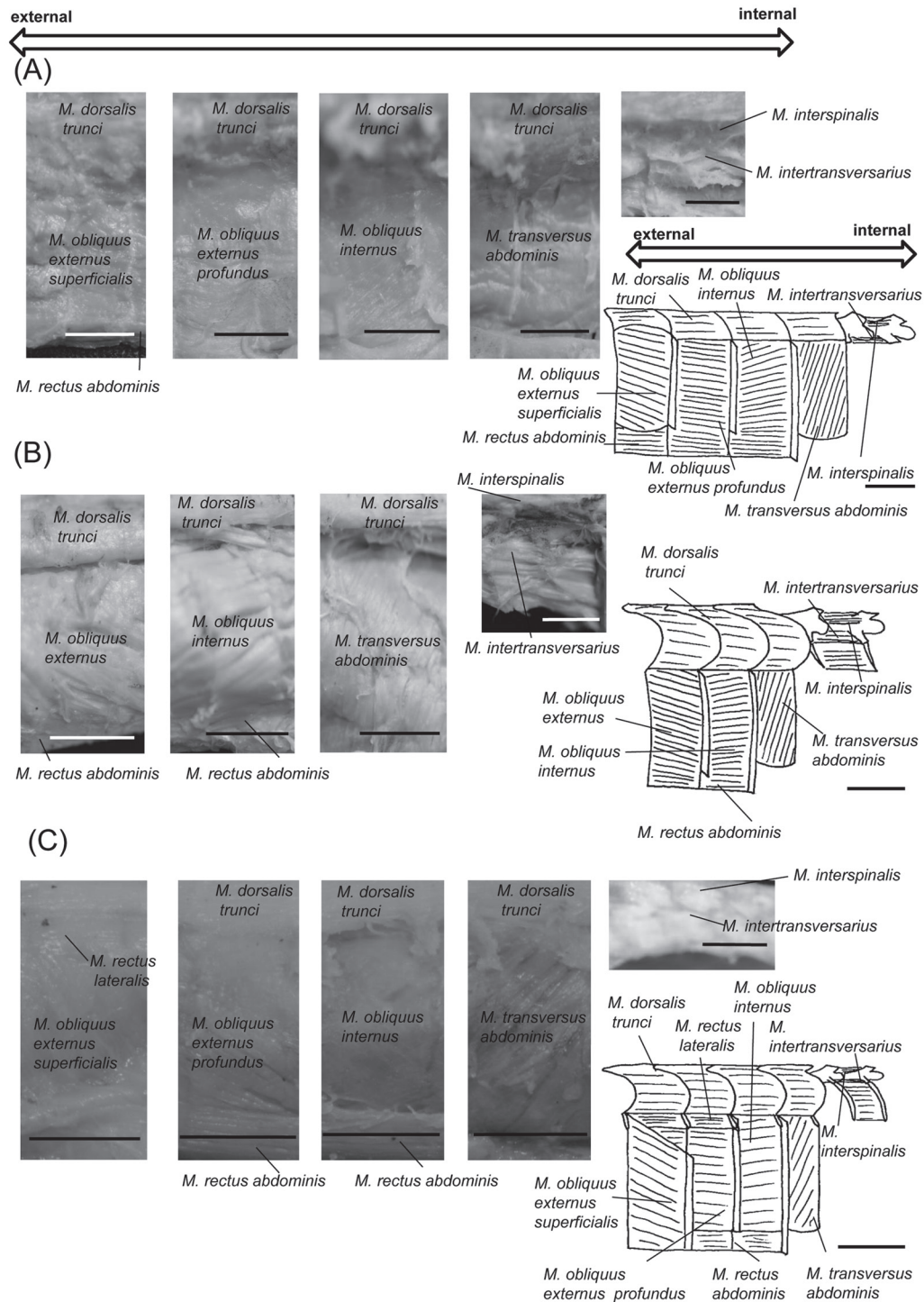
Fig. 2. Cross-sections through the midtrunk of (A): *Amphiuma tridactylum*, (B): *Necturus maculosus*, (C): *Cynops pyrrhogaster*, (D): *Hynobius nigrescens*, (E): *Ambystoma tigrinum*. Scale bar=5 mm.

grouped into lateral hypaxial muscles, and *M. rectus lateralis* is found along the trunk on the lateral hypaxial muscles. *M. rectus abdominis* and *M. rectus profundus* form the ventral abdominal wall.

The following trunk muscles were examined in this study: *M. dorsalis trunci*, *M. interspinalis*, *M. intertransversarius*, *M. subvertebralis*, *M. obliquus externus*, *M. obliquus externus superficialis*, *M. obliquus externus profundus*, *M. obliquus internus*, *M. transversus abdominis*, *M. rectus profundus*, *M. rectus lateralis* and *M. rectus abdominis*. Each trunk muscle on the left side was dissected using tweezers in the five species, and specimens were observed from the lateral view (Fig. 1). Subsequently, cross-sections were

obtained from the middle of the trunk between the pectoral and pelvic girdles on the right side of the body. Images of the lateral view and cross-sections were observed using a microscope with a single-lens reflex camera.

During dissection, specimens were moistened with water to avoid drying, which may cause measurement error. Each trunk muscle was weighed to an accuracy of 0.01 mg using an electronic balance Shimadzu AUW220D (Shimadzu, Kyoto, Japan). The ratio of the weight of each muscle to the weight of all trunk muscles was calculated as a percentage. In this study, to calculate these ratios, the weight of all trunk muscles was treated except that of *M. rectus lateralis*, because of its small size. For distinction among the five



species, values for some muscles were grouped according to anatomical position, running direction and function: *M. obliquus externus superficialis* and *M. obliquus externus profundus*; *M. obliquus internus* and *M. transversus abdominis*; *M. rectus profundus* and *M. rectus abdominis*.

Statistical tests were performed to elucidate the relationship among species. These tests were conducted using statis-

tical processing software (JMP Pro 9, SAS Institute Japan, Tokyo, Japan). Homogeneity of variance and means between species were confirmed by analysis of variance (ANOVA). When significant differences were identified by ANOVA, differences between species were estimated using Tukey's test.

Anatomy: Each trunk muscle was divided as shown in

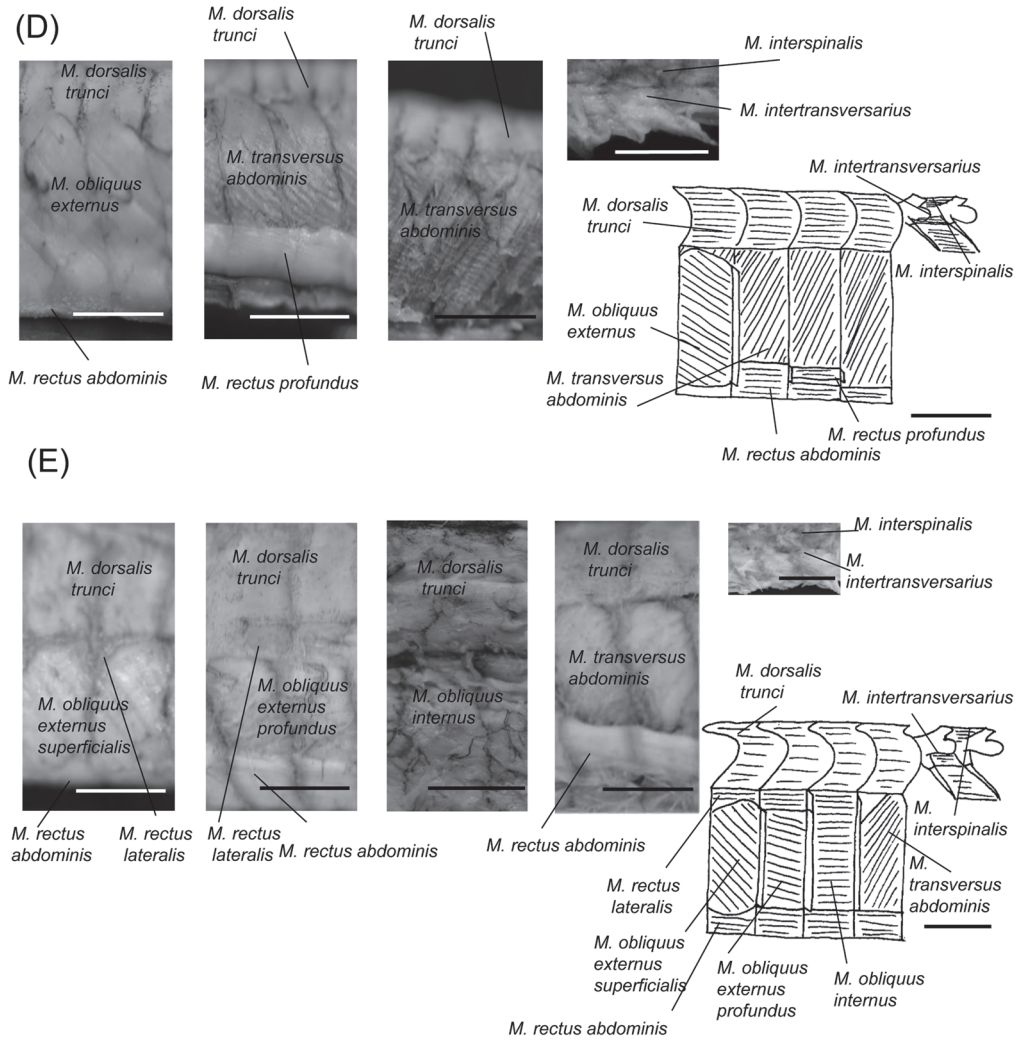


Fig. 3. Lateral view of (A): *Amphiuma tridactylum*, (B): *Necturus maculosus*, (C): *Cynops pyrrhogaster* [right page], (D): *Hybobius nigrescens* [this page], (E): *Ambystoma tigrinum*. Scale bar=5 mm.

Fig. 1. Francis [8], Naylor [14] and Maurer [12, 13] were used as references for the following muscle descriptions. *M. dorsalis trunci* occupies the bulk of the epaxial muscle mass. Muscle fibers run in a longitudinal direction. *M. interspinalis* connects the vertebrae. *M. interspinalis* is situated dorsal and lateral to the vertebrae. *M. intertransversarius* passes between the transverse processes of the vertebrae. *M. rectus lateralis* is found along the trunk on the lateral hypaxial muscles. *M. subvertebralis* is below the vertebrae. Two superficial lateral hypaxial layers consist of *M. obliquus externus superficialis* and *M. obliquus externus profundus*. These muscle fibers run from the craniodorsal region caudo-ventrally towards the pubic bone. *M. obliquus internus* and *M. transversus abdominis* make up the inner lateral hypaxial layers. These muscle fibers run from the cranioventral trunk region to the dorsal parts of the hip girdle.

Some species have *M. obliquus externus* instead of *M. obliquus externus superficialis* and *M. obliquus externus profundus*. *M. obliquus externus* is found in the superficial lateral hypaxial layer. Some species have no *M. obliquus internus*. *M. rectus profundus* lies under the *M. rectus abdominis*. *M. rectus abdominis* forms the ventral body wall. Muscle fibers run in a sagittal direction.

RESULTS

Observations of muscle morphology: Cross-sectional areas and lateral views of the trunk muscles for the five species of salamanders are shown in Figs. 2 and 3, respectively. The number of muscle layers and specialization of each muscle differed by species. In *A. tridactylum*, an aquatic species, four layers (*M. obliquus externus superficialis*, *M. obliquus*

Table 2. Muscle weight ratios (%) measured at midtrunk (mean \pm SEM)

Species	<i>M. dorsalis trunci</i>	<i>M. interspinalis</i>	<i>M. intertransversarius</i>	<i>M. subvertebralis</i>	<i>M. obliquus externus</i> , <i>M. obliquus externus superficialis</i> + <i>M. obliquus externus profundus</i>	<i>M. transversus abdominis</i> , <i>M. obliquus internus</i> + <i>M. transversus abdominis</i>	<i>M. rectus abdominis</i> , <i>M. rectus profundus</i> + <i>M. rectus abdominis</i>
<i>Amphiuma tridactylum</i>	33.3 \pm 0.8 ^c	3.2 \pm 0.4 ^{c,d}	2.1 \pm 0.3 ^c	9.5 \pm 1.3 ^d	23.2 \pm 1.2 ^a	25.0 \pm 1.9 ^a	3.7 \pm 0.4 ^e
<i>Necturus maculosus</i>	34.0 \pm 1.8 ^{b,c}	3.0 \pm 0.5 ^d	2.0 \pm 0.3 ^c	10.4 \pm 0.6 ^{c,d}	20.6 \pm 0.8 ^a	25.8 \pm 2.9 ^a	4.0 \pm 0.8 ^e
<i>Cynops pyrrhogaster</i>	40.0 \pm 1.9 ^b	4.8 \pm 0.4 ^{b,c}	2.6 \pm 0.2 ^{b,c}	13.5 \pm 0.4 ^{b,c}	15.1 \pm 1.8 ^b	14.5 \pm 1.9 ^b	9.4 \pm 0.4 ^b
<i>Hynobius nigrescens</i>	46.4 \pm 2.3 ^a	5.0 \pm 0.3 ^b	3.4 \pm 0.5 ^{a,b}	14.4 \pm 0.5 ^{a,b}	10.4 \pm 2.6 ^e	7.3 \pm 1.2 ^c	13.1 \pm 1.5 ^a
<i>Ambystoma tigrinum</i>	45.7 \pm 3.8 ^a	6.8 \pm 1.2 ^a	3.6 \pm 0.2 ^a	16.9 \pm 2.1 ^a	6.0 \pm 0.4 ^d	7.7 \pm 2.6 ^c	12.3 \pm 0.2 ^a

Different superscript letters indicate significant differences (ANOVA and Tukey's test, $P < 0.05$).

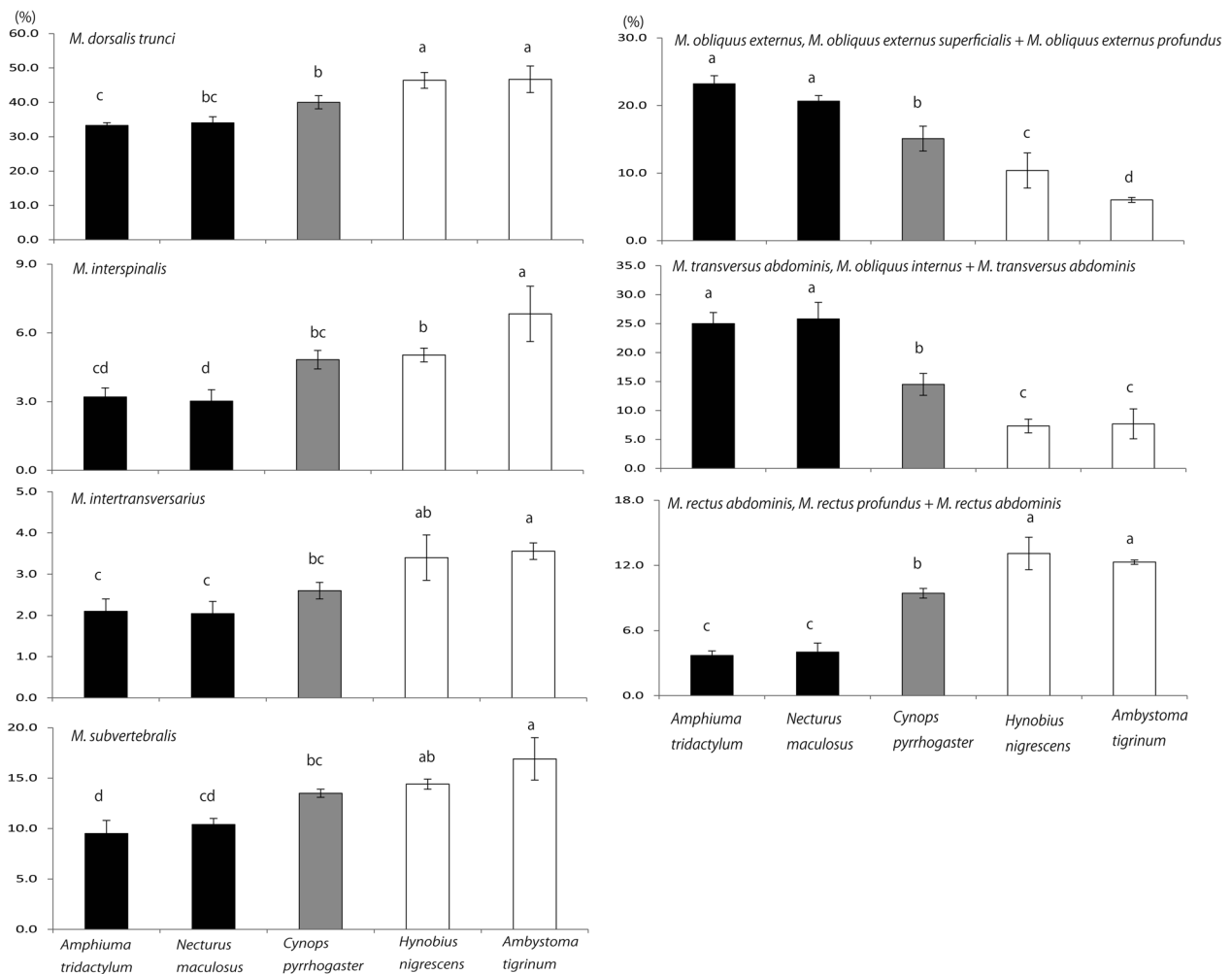


Fig. 4. Muscle weight ratios of each trunk muscle in *A. tridactylum*, *N. maculosus*, *C. pyrrhogaster*, *H. nigrescens* and *A. tigrinum*. Different superscript letters indicate significant differences (ANOVA and Tukey's test, $P < 0.05$). Black bar: aquatic species, gray bar: semi-aquatic species, white bar: terrestrial species.

externus profundus, *M. obliquus internus* and *M. transversus abdominis*) composed the lateral hypaxial musculature. *M. rectus abdominis* in *A. tridactylum* could not be distinguished from *M. obliquus externus profundus* and *M. obliquus internus*. The lateral hypaxial muscles of *A. tridactylum* were

relatively thick and covered the *M. dorsalis trunci*. In *N. maculosus*, an aquatic species, three layers (*M. obliquus externus*, *M. obliquus internus* and *M. transversus abdominis*) made up the lateral hypaxial muscles, which were relatively thick. The *M. rectus abdominis* of *N. maculosus* was not

separated from *M. obliquus externus* and *M. obliquus internus*. The lateral hypaxial muscles of *C. pyrrhogaster*, a semi-aquatic species, consisted of four layers: *M. obliquus externus superficialis*, *M. obliquus externus profundus*, *M. obliquus internus* and *M. transversus abdominis*. The lateral hypaxial muscles of *C. pyrrhogaster* were comparatively thin. *M. rectus abdominis* was easily separated from *M. obliquus externus profundus* and *M. obliquus internus*. *M. rectus lateralis* was observed in *C. pyrrhogaster*. In *H. nigrescens*, a terrestrial species, two layers were evident in the lateral hypaxial muscles: *M. obliquus externus* and *M. transversus abdominis*. Lateral hypaxial muscles of *H. nigrescens* were thin. *H. nigrescens* possessed *M. rectus profundus* and an isolated *M. rectus abdominis*. In *A. tigrinum*, a terrestrial species, four layers (*M. obliquus externus superficialis*, *M. obliquus externus profundus*, *M. obliquus internus* and *M. transversus abdominis*) made up the lateral hypaxial muscles, which were relatively thin. *M. rectus abdominis* of *A. tigrinum* separated from other muscular structures. *M. rectus lateralis* was observed in *A. tigrinum*.

Muscle weight: Weight ratios of trunk muscles to overall muscle weight are represented in Table 2 and Fig. 4. Considerable variations were observed between these salamanders. Significant differences were shown among species in *M. dorsalis trunci* weight ratios [F (4, 10)=22.79, $P<0.01$] ("F" explains F-value of ANOVA, and numbers in bracket mean degrees of freedom). For *M. dorsalis trunci*, weight ratios were smaller in aquatic species (*A. tridactylum* of 33.3% and *N. maculosus* of 34.0%) and significantly smaller than those of terrestrial species ($P<0.05$). For the terrestrial species, *H. nigrescens* and *A. tigrinum*, *M. dorsalis trunci* accounted for more than 46% of muscle weight. Among the more aquatic species, *M. interspinalis* occupied a smaller percentage of total muscle weight than that of more terrestrial species, and significant interspecific differences were demonstrated [F (4, 10)=17.05, $P<0.01$]. In *A. tigrinum*, which is a terrestrial species, *M. interspinalis* made up less than 7% of total muscle weight, but the value for this muscle was significantly larger than that of aquatic species. Significant differences were exhibited among species [F (4, 10)=15.82, $P<0.01$] in *M. intertransversarius* weight ratios. In more aquatic species, *M. intertransversarius* was smaller. The weight ratio of *M. intertransversarius* in *H. nigrescens* and *A. tigrinum* was significantly larger than in aquatic species ($P<0.05$). For *M. subvertebralis*, significant differences in weight ratios among species were shown [F (4, 10)=19.87, $P<0.01$]. In aquatic species, the weight ratio for *M. subvertebralis* was significantly smaller than that of terrestrial species ($P<0.05$).

In contrast, different trends were observed in the lateral hypaxial musculature. Significant interspecific differences in weight ratio of *M. obliquus externus* were seen among species [F (4, 10)=61.20, $P<0.01$]. Weight ratios for *M. obliquus externus* were significantly larger in more aquatic species ($P<0.05$). *M. obliquus externus* weight ratios were significantly larger than 20% in aquatic species (*A. tridactylum* and *N. maculosus*). Significant differences in weight ratios of *M. transversus abdominis* were observed among species [F (4, 10)=51.68, $P<0.01$]. Similarly, in more aquatic

species, weight ratios for *M. transversus abdominis* were larger. In *A. tridactylum* and *N. maculosus*, weight ratios for *M. transversus abdominis* were significantly larger than in other species ($P<0.05$). In terrestrial species (*H. nigrescens* and *A. tigrinum*), *M. transversus abdominis* occupied less than 8% of total muscle weight, a significantly smaller percentage than in other species. Finally, significant differences among species were exhibited in weight ratio for *M. rectus abdominis* [F (4, 10)=90.82, $P<0.01$]; it was smaller in more aquatic species. In aquatic species (*A. tridactylum* and *N. maculosus*), *M. rectus abdominis* accounted for less than 5% of total muscle weight, which was significantly smaller than that in other species ($P<0.05$). Terrestrial species (*H. nigrescens* and *A. tigrinum*) were equipped with significantly larger *M. rectus abdominis*.

DISCUSSION

Morphological trends: A comparison of trunk muscles on cross sections through the midtrunk region showed interspecific variations in relative muscle thickness (Fig. 2). Thicker lateral hypaxial muscles were found in more aquatic species, whereas thinner lateral hypaxial muscles were found in more terrestrial species. This finding supports the results of a previous study by Simons and Brainerd [21] comparing *S. lacertina*, *A. tridactylum*, *Cryptobranchus alleganiensis* and *A. tigrinum*. In the more developed limbs of the terrestrial species, the locomotive function of the lateral hypaxial muscles shifts, and their thickness decreases [18]. *M. obliquus internus*, one of the lateral hypaxial muscles, is used during both swimming and walking [3–5]. In swimming, *M. obliquus internus* mainly produces lateral bending and produces or resists long-axis torsion and produces sagittal flexion [5]. In terrestrial locomotion, *M. obliquus internus* plays a role in counteracting long-axis torsion of the trunk [3–5]. While lateral hypaxial muscles are used on the ground, more aquatic species may need larger lateral hypaxial muscles for lateral bending, because of water viscosity and the resulting drag. Especially in *A. tridactylum*, *M. dorsalis trunci* was partly covered by lateral hypaxial muscles (Fig. 3). Although both *A. tridactylum* and *N. maculosus* are fully aquatic species, *A. tridactylum* possesses smaller limbs than *N. maculosus*. Therefore, *A. tridactylum* may depend more than *N. maculosus* on dorsally enlarged lateral hypaxial muscles for locomotion.

M. rectus lateralis was recognized in *A. tigrinum*, which is a terrestrial species, and *C. pyrrhogaster*, which is a semi-aquatic species, and *M. rectus profundus* was observed in *H. nigrescens*, which is a terrestrial species. Although differences were observed in the number of layers of lateral hypaxial muscles among species, no significant trend was found related to habitat or predominant mode of locomotion. These results are consistent with those of Simons and Brainerd [21] for other taxa. The same authors did not find a close association between ecology and predominant mode of locomotion of salamanders with the number of hypaxial muscle layers in their analysis of ten families of Urodela. A further study of function and phylogeny is needed.

M. rectus abdominis was independent of lateral hypaxial muscles in semi-aquatic species (*C. pyrrhogaster*) and terrestrial species (*H. nigrescens* and *A. tigrinum*). However, *M. rectus abdominis* in aquatic species (*A. tridactylum* and *N. maculosus*) was continuous with the lateral hypaxial musculature. When a muscle separated, its function becomes more specific [11]. Therefore, it is reasonable to assume a more specific function of *M. rectus abdominis* in more terrestrial species. *M. rectus abdominis* plays a role in counteracting sagittal extension of the trunk produced by the action of the epaxial muscles [5, 20] and by the gravity with the elongate trunk in salamanders [17]. Therefore, we suggest that the terrestrial species examined in this study use their relatively greater and clearly isolated *M. rectus abdominis* in resisting sagittal extension of the trunk and that this adaptation is related to the amount of time they spend on land.

Muscle weights: We found *M. dorsalis trunci* was larger in more terrestrial species (Fig. 4). During both swimming and walking, *M. dorsalis trunci* produces lateral bending [5, 6, 9]. In addition, most lateral strands of the autochthonous *M. dorsalis trunci* may be in a position to exert ventral flexing of the trunk (Fig. 2). To keep the vertebral column, this is needed. A stabilizing function for epaxial muscles was proposed in O'Reilly *et al.* [16]. Therefore, in order to counteract the effect of gravitational forces, *M. dorsalis trunci* was greater in more terrestrial species. *M. interspinalis* was also heavier in more terrestrial species (Fig. 4). *M. interspinalis* may also contribute to flexing the trunk ventrally to counteract the influence of the gravity by its position (Fig. 2). Thus, *M. interspinalis* was larger in more terrestrial species, which employ *M. interspinalis* on land.

M. intertransversarius was also larger in more terrestrial species (Fig. 4). Although the function of *M. intertransversarius* has not been clarified, it seems to play a role in ensuring spinal integrity and ventral flexing similar to *M. interspinalis*, because of its location between vertebrae. *M. subvertebralis* was also greater in more terrestrial species (Fig. 4). Functional subunits that can stabilize and mobilize the trunk and adjust body stiffness compose *M. subvertebralis* [19]. In addition, *M. subvertebralis* may play a role in ventral flexing against gravity. Because of its role in trunk stabilization, *M. subvertebralis* is more often utilized in terrestrial environments. Thus, heavier *M. subvertebralis* is characteristic of more terrestrial species.

Lateral hypaxial muscles (*M. obliquus externus superficialis*, *M. obliquus externus profundus*, *M. obliquus internus* and *M. transversus abdominis*) were larger in more aquatic species (Fig. 4). Lateral hypaxial muscles function in torsion control and maintaining stability [3, 5]. As mentioned earlier, lateral hypaxial muscles are used in both swimming and walking [3–5]. *M. obliquus internus* has functions of mainly producing lateral bending and producing or resisting long-axis torsion of the trunk as well as some sagittal flexion in swimming [5]. In terrestrial locomotion, *M. obliquus internus* plays a role in counteracting long-axis torsion of the trunk [3–5]. Trunk muscles in species with diminutive limbs produce lateral bending actively during aquatic locomotion, whereas lateral bending is produced passively by the muscle

action of extrinsic limbs [20]. More developed limbs are used in forward movement on the ground. Aquatic species rely more on lateral bending of the trunk to move forward; therefore, weights of lateral hypaxial muscles are relatively greater in more aquatic species. Though all lateral hypaxial muscles play a role in stabilization and torsion control on ground, muscle ratios of lateral hypaxial muscles may be affected by differences in lateral bending in different environments.

Since muscular forces along the ventral contour line are needed in animals with lengthy trunks that are supported by limbs [17], the *M. rectus abdominis*, which is the most ventral muscle, must be heavier in more terrestrial species [5, 17]. It is suggested that the function of *M. rectus abdominis* is to prevent sagittal trunk extension caused by the action of the epaxial muscles [5] and by the gravity with the elongate trunk in salamanders [17]. Since larger weight ratios for *M. dorsalis trunci* were observed in more terrestrial species (Fig. 4) and influence of gravity occurs [17], dorsally concave curvature of the trunk by dorsal muscles may also be larger than in more aquatic species. To resist greater dorsally concave curvature of the trunk, larger *M. rectus abdominis* is necessary in more terrestrial species.

Specimens used in this study differed in size. The aquatic species were larger than the terrestrial species, and lateral hypaxial muscles were thicker and heavier in the aquatic forms. It is considerable that the stronger development of the lateral hypaxial musculature in the aquatic species may be enforced by the factor by size.

In this study, interspecific variation in trunk musculature among Urodela reflects their main mode of locomotion in different ecological habitats. The results of this study may improve our understanding of basal vertebrate locomotion.

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