

Morphology and Function of Lateral Hypaxial Musculature in Salamanders¹

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SYNOPSIS. The lateral hypaxial musculature (LHM) of salamanders may serve as a useful model for understanding the functions of LHM in tetrapods more generally. Salamanders have between two and four layers of LHM, arranged segmentally in myomeres. These layers produce three primary mechanical actions: they bend the body, pressurize the body, and produce or resist torsion about the long axis of the body. The optimum muscle fiber angle for forceful bending is 0° to the long axis, the optimum angle for pressurization is 90°, and the optimum angle for torsion is 45°. For generating bending and torsional moments, lateral (superficial) muscle layers have greater mechanical advantage than medial (deep) layers. For increasing body pressure, by contrast, medial layers have greater mechanical advantage. A comparison of muscle fiber angles in aquatic and terrestrial salamanders reveals that some aquatic salamanders have one muscle layer with a low fiber angle which may represent a specialization for swimming. Overall, however, the fiber angles in the LHM of terrestrial and aquatic salamanders are surprisingly similar. In contrast, the pattern of fiber angles in caecilians is different, suggesting that these amphibians use their LHM differently. The fiber angle models and morphological observations presented here form a framework which may be useful in future studies of lateral hypaxial musculature.

INTRODUCTION

The lateral hypaxial musculature (LHM) of tetrapods serves many biological roles. In undulatory locomotion, the LHM, along with the epaxial musculature, contributes to lateral bending of the body (Carrier, 1993; Frolich and Biewener, 1992; Gasc, 1974). In lung ventilation, the LHM contributes to forced exhalation in all tetrapods, and the intercostal portions rotate the ribs for aspirational breathing in amniotes (Brainerd and Monroy, 1998; Carrier, 1989). During terrestrial walking and trotting, the function of the LHM is more uncertain. Some studies indicate that the primary function of the LHM is to stabilize the body against ground reaction forces (Carrier, 1990, 1996), whereas others suggest that the primary function is to produce lateral bending (Ritter, 1995, 1996). In addition, the LHM serves a variety of roles in which pressurization of the body cavity is important, such as defecation, vomiting, and oviposition

(Naitoh and Wassersug, 1992; Naitoh *et al.*, 1989).

The lateral hypaxial musculature of salamanders may serve as a useful model for understanding the functions of LHM in tetrapods more generally. In salamanders, the structure of the LHM is considerably simpler than in amniotes (Maurer, 1911; Naylor, 1978; Simons and Brainerd, 1999). Most amniotes have long ribs, and parts of the LHM have become specialized as intercostal muscles. In salamanders, however, the ribs are short and dorsally located, and the LHM does not attach to them. In addition, little specialization of the musculature along the cranio-caudal body axis is present in salamanders. Myomeres closest to the girdles are slightly different in shape and muscle fiber angle, but all of the intervening myomeres are nearly identical (Carrier, 1993; Maurer, 1911).

Two, three or four layers of LHM are present in salamanders, with different muscle fiber angles in each layer (Fig. 1). The layers are generally arranged in segments separated by myosepta, but in some species the *M. transversus abdominis* is unsegmented (Carrier, 1993; Maurer, 1911).

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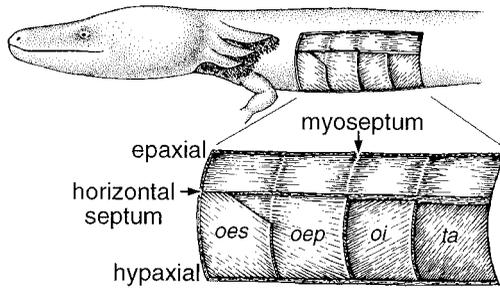


FIG. 1. Axial musculature of an aquatic salamander, *Necturus maculosus*. The layers of lateral hypaxial musculature are exposed from superficial to deep in the cranial to caudal direction. The number of external oblique layers varies between one and two in this species (the figured specimen exhibits two). Abbreviations: oes, *M. obliquus externus superficialis*; oep, *M. obliquus externus profundus*; oi, *M. obliquus internus*; ta, *M. transversus abdominis*. (After Brainerd *et al.*, 1993).

When four layers are present, they are generally called *M. obliquus externus superficialis* (OES), *M. obliquus externus profundus* (OEP), *M. obliquus internus* (OI) and *M. transversus abdominis* (TA). In the two external layers, the muscle fibers run from craniodorsal toward caudoventral, and in the two internal layers, the fibers run from cranioventral toward caudodorsal (Fig. 1).

The functional morphology of the LHM in salamanders has been studied during lung ventilation and during aquatic and terrestrial locomotion (summarized in Table 1). Studies of lung ventilation in several species have shown that the TA is active during exhalation to increase body pressure and drive air out of the lungs (Brainerd, 1998; Brainerd *et al.*, 1993; Brainerd and Dumka, 1995; Brainerd and Monroy, 1998). Sometimes other layers of the LHM contribute to exhalation, but the TA is the primary expiratory muscle. The lungs are then reinflated with a buccal pump.

Electrical activity of the LHM during aquatic and terrestrial locomotion has been studied in one salamander, *Dicamptodon ensatus* (Carrier, 1989). During swimming, all four layers of LHM were found to be active on one side of the body to produce lateral undulation. During walking, external layers and internal layers on contralateral sides of the body were active in synchrony. (For example, the left OES and OEP were

TABLE 1. Functions of lateral hypaxial musculature in salamanders.

Biological roles	Mechanical actions	# of layers active
aquatic locomotion ¹	bending	4
terrestrial locomotion ¹	torsion stabilization	2
exhalation ²	pressurization	1
vomiting ³ , defecation, oviposition, posture	pressurization	— ⁴

¹ Carrier, 1993; ² Brainerd *et al.*, 1993; Brainerd, 1998; Brainerd and Monroy, 1998; ³ Naitoh *et al.*, 1989; Naitoh and Wassersug, 1992; ⁴ not known.

active at the same time as the right OI and TA.) This pattern is consistent with a hypothesis that the primary role of these muscles during walking is to stabilize the trunk against torsional forces created by the diagonal gait of the salamanders.

The above examples indicate that salamanders are able to activate the individual layers of the LHM independently. The layers are activated all together during swimming, in pairs during walking, and singly during exhalation of air from the lungs (Table 1).

The different activation patterns and mechanical actions of these layers suggest that salamanders which are specialized for aquatic or terrestrial locomotion might exhibit quite different morphological patterns in their LHM. For example, the muscle fiber angles within the layers or the presence or absence of some layers might be correlated with locomotor type. The purpose of this paper is to present a theoretical model of the optimum muscle fiber angles for different mechanical actions, and then to employ this model to interpret LHM morphology in phylogenetically and ecologically diverse salamanders.

THEORETICAL MODEL OF OPTIMUM FIBER ANGLES

The lateral hypaxial musculature of salamanders performs three primary mechanical actions: 1) bending the body; 2) resisting or producing torsion about the long axis of the body; and 3) compressing the body, thereby increasing internal pressure (Table 1). Each of these actions is associated with a different optimum muscle fiber angle for greatest mechanical advantage in force pro-

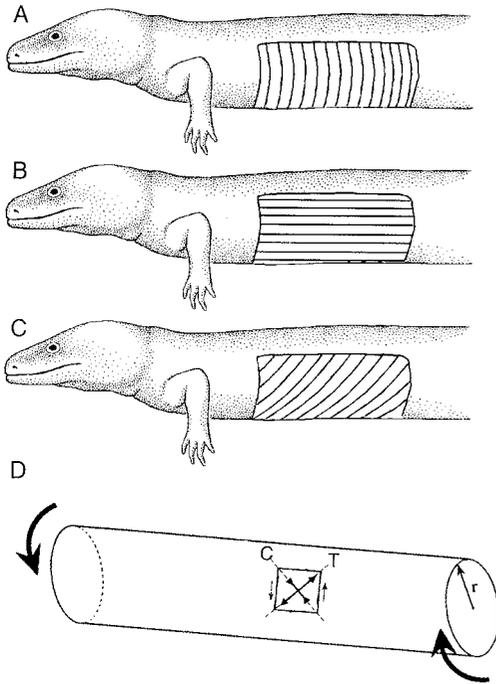


FIG. 2. Idealized optimum muscle fiber angles for the three primary mechanical actions of lateral hypaxial musculature in salamanders. A. Optimum angle for body pressurization. B. Optimum angle for forceful body bending. C. Optimum angle for torsion resistance or production. D. Engineering model of a cylinder in torsion (r is radius, T is principle axis of tension and C is principle axis of compression.)

duction (Fig. 2). For body compression, the optimum fiber angle is 90° to the long axis of the body. In this configuration, the smallest volume of muscle would need to be activated to achieve a given increase in body pressure. For lateral bending, the optimum fiber angle for force production is 0° to the long axis of the body. For torsion production or resistance, the optimum angle is 45° . The reason for this optimum torsion angle becomes clear if we model the body as a cylinder which is subjected to twisting about its long axis (*i.e.*, torsion; Fig. 2D). In this case, the surface of the cylinder will experience principle axes of tension and compression at 45° to the long axis, and muscle fibers oriented along these principle axes will have the optimum fiber angle to produce or resist this torsion.

Only muscle fibers oriented at 90° or 0° will produce a single mechanical action. All

intermediate angles will contribute to all three actions, but in various degrees. A fiber angle of 45° will generate both pressurization and bending of the body, as well as being optimal for torsion resistance. Any collateral forces generated by intermediate fiber angles will need to be balanced internally. Imagine, for example, a salamander with one external layer in which the muscle fibers run from craniodorsal toward caudoventral and one internal layer in which the fibers run from cranioventral toward caudodorsal. In both layers, the fibers form an angle of 45° to the longitudinal axis of the body. During swimming, the animal activates both layers on one side. Its body will bend toward the side of the active muscles, and the torsional forces will be balanced if the two layers are generating equal and opposite torsional moments. If these moments are not balanced, then the body will twist as well as bend, and the animal will not swim in a straight line.

Intermediate fiber angles also affect the speed and force of myomere shortening during lateral bending. At 45° vs. 0° , twice as much muscle will need to be activated to generate a given bending force, but the speed of bending will be increased. As muscle fiber angles increase from 0° to about 50° , there is a trade-off between the bending force that the muscle produces and the shortening velocity of the myomere (much like increasing the length of the output lever arm in a simple lever system). Thus, muscle fibers oriented at 45° will produce relatively weak but rapid shortening of the myomere (Alexander, 1969; E. L. B., unpublished data).

The mechanical actions of the muscle fibers also depend on their positions relative to the vertebral centra. Most of the LHM in salamanders is located ventral to the vertebral centra, and therefore will tend to bend the body in the sagittal plane (Fig. 3). If a salamander is to swim straight, the action of these muscle fibers must be balanced by muscle fibers dorsal to the vertebral centra, presumably in the epaxial musculature. Conversely, all epaxial forces must be balanced by hypaxial forces, and the *M. rectus abdominis* is probably important in this role (D. Homberger, personal communication).

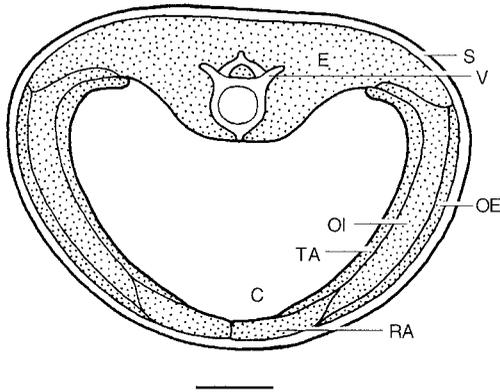


FIG. 3. Transverse section through the mid-trunk region of *Cryptobranchus alleganiensis*. Abbreviations: C, coelom; E, epaxial musculature; OE, *M. obliquus externus*; OI, *M. obliquus internus*; R, *M. rectus abdominis*; TA, *M. transversus abdominis*, S, skin; V, vertebra. (After Simons and Brainerd, 1999).

Mediolateral position also affects the mechanical advantage of the muscle layers. A more superficial (lateral) muscle layer will have greater mechanical advantage in bending and torsion than a deeper (more medial) layer because its line of action is more distant from the vertebral column. In contrast, for generating internal body pressure (compression), more medial layers have greater mechanical advantage. If we think of the body as a thin-walled cylinder with a radius (r) which is pressurized by an external layer of muscle of thickness (h) which generates a tension (T), then the pressure (P) inside the cylinder is inversely related to the radius, $P = Th/r$ (Wainwright *et al.*, 1976). Therefore, the pressure that transversely oriented muscles can generate is inversely related to their distance from the center of the body.

Variability in the dorsoventral and mediolateral positions of the muscle fibers adds complexity to our model of the LHM, but we still expect our predictions of optimum muscle fiber angles for forceful bending, pressurization, and torsion to hold true. Salamanders occupy a range of habitats from terrestrial to fully aquatic, and it is reasonable to suspect that the LHM of aquatic and terrestrial species might exhibit differences in fiber angle that would indicate differences in the primary mechanical actions of the layers. From Carrier's (1989)

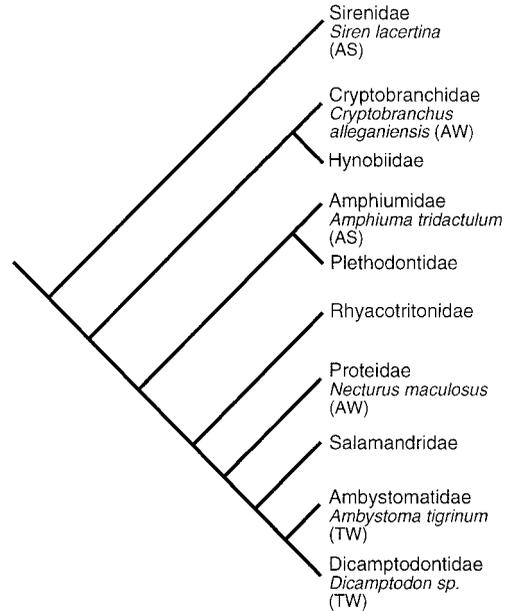


FIG. 4. Phylogenetic relationships and ecotypes of study species. Genus and species name for our six study species are given below their respective families, and ecotype is indicated (TW, terrestrial walker; AW, aquatic walker; and AS, aquatic swimmer). Phylogenetic relationships from Larsen and Dimmick (1993).

work on *Dicamptodon*, we would expect that torsion control would be the most important action of LHM in terrestrial salamanders. Therefore we predict that terrestrial salamanders will maintain fiber angles near 45° for maximum torsion control.

In contrast, aquatic salamanders do not experience torsion due to ground reaction forces because the body weight of aquatic swimmers and walkers is supported primarily by buoyancy (although hydrodynamic forces could induce transient torsional moments). Therefore, relative to terrestrial walkers, we expect that the fiber angles of aquatic swimmers and walkers may be less constrained to 45° . In aquatic salamanders, we predict that one or more layers will be specialized for producing forceful lateral bending (fiber angles near 0°) and one or more layers will be specialized for body pressurization (fiber angles close to 90°).

MUSCLE FIBER ANGLES IN THREE ECOTYPES

We tested the above predictions by measuring fiber angles in the lateral hypaxial

musculature of six salamanders representing six families and three different ecotypes: terrestrial walkers, aquatic walkers, and aquatic swimmers (Fig. 4). Terrestrial walkers were represented by *Dicamptodon* sp. and *Ambystoma tigrinum* which both have short bodies and robust limbs. Aquatic walkers were represented by *Necturus maculosus* and *Cryptobranchus alleganiensis* which have somewhat elongated bodies and fairly robust limbs. These salamanders are good swimmers, but they are also able to walk underwater on the bottom. Aquatic swimmers were represented by *Amphiuma tridactylum* and *Siren lacertina* which have elongated bodies and highly reduced limbs.

We dissected the LHM of three individuals from each of the six species, and used a camera lucida to draw the fiber angle of at least ten fibers per muscle layer (see also Simons and Brainerd (1999) for more detailed morphological analysis of the muscle layers). Results from the three individuals are shown as differently patterned bars in Fig. 5. In order to facilitate comparison among layers, all angles were measured as acute angles relative to the horizontal axis of the body. Three of the six species were found to have only one external oblique layer, *M. obliquus externus*, and three were found to have two external layers, *M. obliquus externus superficialis* and *M. obliquus externus profundus*. Intraspecific variation in the number of external oblique layers was observed in *S. lacertina* and *N. maculosus*, as will be discussed below.

A general pattern of the relative angles between layers emerges from Fig. 5. The most lateral (OE or OES) layer and the most medial layer (TA) tend to have higher angles than the middle layers (OEP and OI). This pattern can also be seen in Fig. 1; fibers in the OES and the TA are nearly transverse and fibers in the EOP and OI are nearly longitudinal.

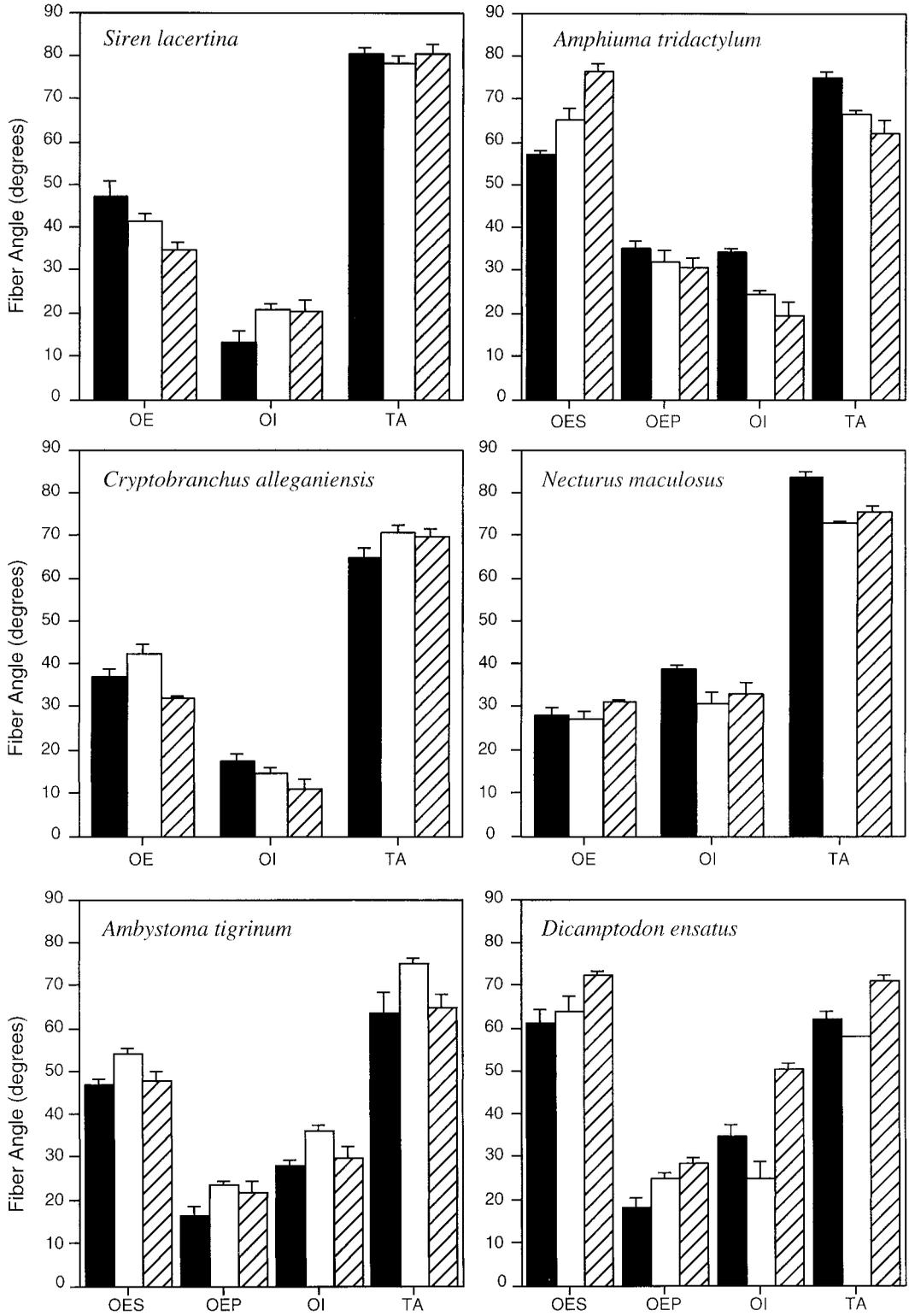
In all species examined, fibers of the TA are oriented at high angles, often the highest of any of the layers (Fig. 5). The transverse orientation of the TA gives this muscle good mechanical advantage for compressing the body and increasing body pressure. The high fiber angle of the TA is also consistent with its medial position relative

to the rest of the LHM. As mentioned above, the mechanical advantage of a transversely oriented muscle layer is inversely related to its radial distance from the center of the body. Therefore, the effectiveness of the TA is increased by its medial location, whereas the effectiveness of obliquely or longitudinally oriented layers would be decreased. These observations are consistent with the finding that the TA is the primary muscle used to increase body pressure and force air out of the lungs during exhalation (Brainerd, 1998; Brainerd *et al.*, 1993; Brainerd and Monroy, 1998). It is also likely that the TA participates in other functions for which body compression is important, such as defecation and emesis (Table 1).

The high fiber angle of the TA may explain why this muscle is unsegmented in some salamanders. Muscle fibers oriented at a very high angle cannot originate and insert on the myosepta. Instead, they originate from an aponeurosis that is continuous with the epimysium of the epaxial musculature and insert onto an aponeurosis that merges with the peritoneum (Simons and Brainerd, 1999). Therefore, myosepta are sometimes absent from the TA or are oriented in a different direction from the myosepta of the more superficial layers (Maurer, 1911; Naylor, 1978).

The above arguments do not hold true for the OES layer, which also exhibits a very high fiber angle. The OES is the most lateral layer, and it is usually segmented even though in many species few of the muscle fibers actually insert onto the myosepta (for example, see Carrier, 1993). Within our current framework, the structure and function of this layer are puzzling.

No large or consistent differences in fiber angles corresponding with ecotypes were found (Fig. 5). For example, the angles for an elongate aquatic swimmer, *Amphiuma*, were very similar to the angles for a highly terrestrial salamander, *Dicamptodon*. We predicted that in animals that swim, at least one layer would have angles near 0° as a specialization for lateral undulation. In both *Siren* and *Cryptobranchus*, the OI exhibits low fiber angle as predicted (means of 18 and 14°), but in *Necturus* (mean of 34°), the OI is not more longitudinal than in the ter-



restrial walkers, *Ambystoma* and *Dicamptodon* (means of 32 and 27°). The OI of *Amphiuma* is intermediate, with a mean angle of 24°. Thus, although we did not find a large and consistent difference between aquatic and terrestrial species, we did observe a tendency for the OI to have a lower fiber angle in aquatic species.

A surprising amount of intraspecific variation in fiber angles was observed. In some cases, the range of intraspecific variation is almost as large as the range of mean interspecific variation. For the TA, the largest interspecific difference is 16°, observed between *Siren* (mean of 80°) and *Dicamptodon* (mean of 64°). We observed intraspecific differences in the TA that were almost as large (12° in *Dicamptodon* and *Amphiuma*). For the OI, the largest interspecific difference is 23°, observed between *Cryptobranchus* (mean of 14°) and *Dicamptodon* (mean of 37°). The intraspecific difference in *Dicamptodon* was 23°, but differences within other species were smaller. We are confident that these intraspecific differences are not due to measurement artifacts. We dissected both sides of several different individuals, and found similar values from both dissections.

The general pattern of fiber angles observed in salamanders can be compared with fiber angles measured in another group of amphibians, the Gymnophiona (caecilians; Fig. 6). The pattern of relative fiber angles is quite different in caecilians, even when compared with elongate, nearly limbless salamanders such as *Amphiuma* and *Siren* (for LHM morphology in caecilians, see Naylor and Nussbaum, 1980; Nussbaum and Naylor, 1982). Caecilians show muscle layers with angles of 0° and 90° (OEP and TA), indicating that these muscles act only to produce bending and pressurization of the body. The other two layers show angles

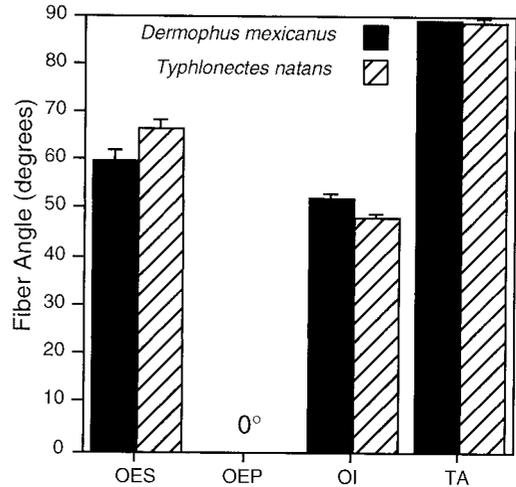


FIG. 6. Muscle fiber angles in caecilians. Angles in one individual from each of two species, *Dermophis mexicanus* (solid bars) and *Typhlonectes natans* (hatched bars), are shown. At least ten fibers per muscle layer per individual were measured; error bars indicate standard error of these repeated measurements. All angles were measured as acute angles to the horizontal axis of the body. Abbreviations: OES, *M. obliquus externus superficialis*; OEP, *M. obliquus externus profundus*; OI, *M. obliquus internus*; TA, *M. transversus abdominis*.

of 50–60° as would be predicted by the hydrostatic skeleton model of internal concertina locomotion in caecilians (O'Reilly *et al.*, 1997). It is unclear, however, how these oblique layers interact with the transverse and longitudinal layers during locomotion.

PRESENCE AND ABSENCE OF LAYERS

Considerable variation in the number of layers present in the lateral hypaxial musculature of salamanders has been observed (Naylor, 1978; Simons and Brainerd, 1999). Salamanders may have two, three or four layers of LHM, but at least one external layer, in which the fibers run from craniodorsal toward caudoventral, and one inter-

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FIG. 5. Muscle fiber angles in the lateral hypaxial musculature of six salamander species representing three ecotypes (top panels, aquatic swimmers; middle panels, aquatic walkers; bottom panels, terrestrial walkers). The three patterned bars for each muscle layer represent three different individuals. At least ten fibers per muscle layer per individual were measured; error bars indicate standard error of these repeated measurements. All angles were measured as acute angles to the horizontal axis of the body. Abbreviations: OES, *obliquus externus superficialis*; OEP, *obliquus externus profundus*; OE, *obliquus externus*; OI, *obliquus internus*; TA, *transversus abdominis*.

TABLE 2. Presence and absence of lateral hypaxial layers within one family of salamanders (Salamandridae). This table reports results for 16 species; it is not a complete survey of all salamandrids. (Data compiled from Naylor, 1978).

Pattern	Layers	sp.	External layers			Internal layers		
A	4	8	oes	—	oep	oi	—	ta
B	3	3	oes	—	oep	—	oi/ta	—
C	3	1	—	oe	—	oi	—	ta
D	2	4	—	oe	—	—	oi/ta	—

Abbreviations: sp., number of species examined exhibiting each pattern; oes, obliquus externus superficialis; oep, obliquus externus profundus; oe, obliquus externus (no separation of external layers); oi, obliquus internus; ta, transversus abdominis; oi/ta, obliquus internus/transversus abdominis (no separation of internal layers).

nal layer, in which the fibers run from cranioventral toward caudodorsal, are always present. Thus, there are four possible patterns in which the layers may be present or absent (Table 2).

Remarkably, some families, such as Salamandridae and Hynobiidae, exhibit extensive variability in layer number, whereas others, such as Plethodontidae, exhibit little (Naylor, 1978; Simons and Brainerd, 1999). Within the salamandrids, for example, all four possible combinations of layers are present (Table 2). Indeed, variation is high even within some genera. The genus *Tri-*

turus exhibits three of the four patterns (A, C and D).

We also observed some intraspecific variation in the presence and absence of layers. Three of five *Siren lacertina* that we dissected had only one external layer, and two had two external layers. Three *Necturus maculosus* were found to have only one external layer, and another researcher has also found specimens with one external oblique (D. Homberger, personal communication). However, two external layers were observed in previous studies (Brainerd *et al.*, 1993; Maurer, 1911).

For *Siren* and *Necturus*, we measured muscle fiber angles from individuals with one layer and from individuals with two layers (Fig. 7). These results suggest that whenever there is only one external layer, the single layer has a fiber angle which is intermediate between the angles of two layers. We have also found this to be true in interspecific comparisons (Simons and Brainerd, 1999). Species with only one external or internal layer tend to have fiber angles that are intermediate between species which have two.

We were surprised to find variation in the number of layers at such low phylogenetic levels (within species and genera). One might expect that the presence or absence of layers would have a significant impact on the mechanical capabilities of the LHM. More layers with divergent fiber angles should provide more precise control over the action of the LHM as a whole. Conversely, the presence of fewer layers should simplify motor control for species which might require less fine control over their LHM. However, counts of layer number in

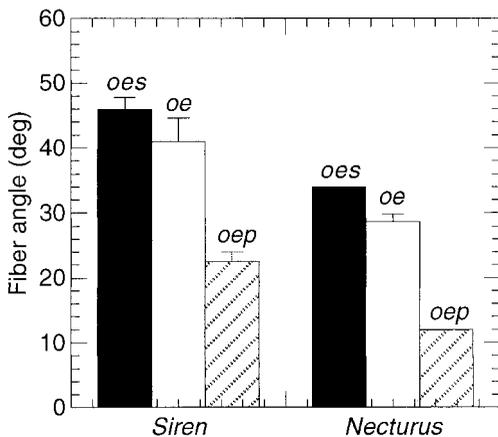


FIG. 7. Muscle fiber angles in the external layers of *Siren lacertina* and *Necturus maculosus*. Some individuals have two external layers and some have only one. Three *Siren* with one layer were measured (n = 3; SE for three individuals shown) and two *Siren* with two layers were measured (n = 2). Three *Necturus* with one layer were measured (n = 3) and results from one *Necturus* with two layers were taken from Brainerd *et al.* (1993). Abbreviations: oes, obliquus externus superficialis; oep, obliquus externus profundus; oe, obliquus externus.

57 salamander species revealed no obvious correlation between number of layers and ecotype (Naylor, 1978; Simons and Brainerd, 1999). Given our finding that the number of layers can vary within species and within genera, it seems likely that one layer with an intermediate fiber angle functions in much the same way as two layers with divergent fiber angles.

It may be that the presence or absence of layers is a highly developmentally plastic character. Many salamanders have four layers of LHM during larval life, and then lose layers during metamorphosis and have only two or three as adults (Naylor, 1978). The early development of the layers is undescribed, but it is likely that a single external layer divides to form the OES and OEP and that a single internal layer divides to form the OI and TA (Noble, 1931). Given how little we know about the ontogeny of these layers, the homology of single and double layers is uncertain. Quite sensibly, most authors call a single external layer *M. obliquus externus*, but call a single internal layer either *M. obliquus internus* or *M. transversus abdominis*, with no justification for using one or the other. For this reason, we have chosen to call a single internal layer *M. obliquus internus/transversus abdominis*, with no assumption of homology with one layer or the other (Table 2).

CONCLUSIONS

The lateral hypaxial musculature of salamanders is less complex than that of amniotes, but it is more complex and variable than has been previously appreciated. A theoretical model of optimum muscle fiber angles for different mechanical actions provides some insight into the function of layers that have angles near 0° or 90°. However, layers with intermediate angles contribute to all three primary mechanical actions (bending, pressurization, torsion); therefore the functions of these layers are more difficult to interpret. Furthermore, a trade-off exists between optimum fiber angles for forceful versus fast lateral bending. Fiber angles near 0° produce the most forceful lateral bending, but higher fiber angles produce more rapid shortening of the myomeres.

Large intraspecific differences in muscle fiber angles were observed, and interspecific differences were not consistently correlated with aquatic or terrestrial lifestyle (although aquatic salamanders tend to have one layer with low fiber angles). Caecilians exhibit a different pattern of fiber angles from salamanders, indicating that their internal concertina mode of locomotion requires different mechanical actions from the LHM. Intra- and interspecific variation in the number of layers was observed, suggesting that one layer with an intermediate fiber angle can function in much the same way as two layers with divergent fiber angles. Although this study has probably generated more questions than it has answered, we hope that it will stimulate further work on the LHM of salamanders, which may in turn provide some general insight into the function of segmented axial musculature in other vertebrates.

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