

The Evolution of the Functional Role of Trunk Muscles During Locomotion in Adult Amphibians¹

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SYNOPSIS. The axial musculature of all vertebrates consists of two principal masses, the epaxial and hypaxial muscles. The primitive function of both axial muscle masses is to generate lateral bending of the trunk during swimming, as is seen in most fishes. Within amphibians we see multiple functional and morphological elaborations of the axial musculature. These elaborations appear to be associated not only with movement into terrestrial habits (salamanders), but also with subsequent locomotor specializations of two of the three major extant amphibian clades (frogs and caecilians). Salamanders use both epaxial and hypaxial muscles to produce lateral bending during swimming and terrestrial, quadrupedal locomotion. However during terrestrial locomotion the hypaxial muscles are thought to perform an added function, resisting long-axis torsion of the trunk. Relative to salamanders, frogs have elaborate epaxial muscles, which function to both stabilize and extend the iliosacral and coccygeosacral joints. These actions are important in the effective use of the hindlimbs during terrestrial saltation and swimming. In contrast, caecilians have relatively elaborate hypaxial musculature that is linked to a helix of connective tissue embedded in the skin. The helix and associated hypaxial muscles form a hydrostatic skeleton around the viscera that is continuously used to maintain body posture and also contributes to forward force production during burrowing.

INTRODUCTION

Studies of locomotion in tetrapods are heavily biased towards the role of the limbs. However, even when the limbs and their associated musculature are the primary engines of locomotion, the axial muscles perform the critical roles of maintaining posture and transmitting forces between the limbs and the body axis. Furthermore, limb reduction has occurred independently many times during tetrapod evolution (*e.g.*, Greer, 1991) and often leads to the exclusive use of axial muscles to power locomotion (Gray, 1968; Gans, 1985, 1986).

The goal of this paper is to review the functional roles played by amphibian trunk

muscles during locomotion and to identify transitions in these roles that have taken place during amphibian evolution. Living amphibians possess several characteristics that make them an interesting group in which to examine the evolution of the axial musculoskeletal system. Among living tetrapods, salamanders are regarded as most closely resembling the first terrestrial vertebrates, and are therefore considered illustrative of "basal tetrapods." Relative to salamanders, both frogs and caecilians exhibit extremely divergent anatomical and functional specializations of the axial musculoskeletal system, which correspond to their unique modes of locomotion. Therefore, an understanding of the locomotor function of the axial musculoskeletal system of amphibians provides information concerning both the basal characteristics of Tetrapoda and two interesting case studies to test the general hypothesis that muscle function tends to be conserved during evolution.

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Living amphibians consist of three clades with unclear evolutionary relationships (Carroll, 1988; Trueb and Cloutier, 1991a). Caudata (salamanders) are found throughout the Northern Hemisphere and in the northern neotropics. Approximately 400 species are currently recognized, with the majority contained within Plethodontidae (Frost, 1985). Anura (frogs) are found throughout the world with the exception of Antarctica and some mid-oceanic islands. Approximately 4,000 species are currently recognized (Frost, 1985). Lastly, Gymnophiona (caecilians) are found throughout the humid tropics with the exception of Madagascar and Australasia south of Wallace's line. Approximately 150 species of caecilians are currently recognized, but the systematic relationships within this group are still very poorly understood. Most of the described species are currently placed in Caeciliidae (Frost, 1985; Nussbaum and Wilkinson, 1989).

In this paper each of these clades is treated separately. The usual methods of locomotion are discussed, with particular attention to those modes that rely heavily or exclusively on axial musculature. The anatomy and function of the axial muscles is described as far as is known, and especially promising areas for future investigation are proposed. Finally, we reconstruct the most probable ancestral arrangement of the lissamphibian trunk and trace the evolution of axial muscle function within amphibians.

SALAMANDERS

Adult salamanders may be aquatic, semi-aquatic or terrestrial in their habits, and many otherwise terrestrial species seasonally enter water to breed. In water, they both walk along the bottom and swim in the water column. Swimming in salamanders is similar to the undulatory swimming described for elongate fishes (Gray, 1933, 1968). Traveling waves are propagated posteriorly along the body, increasing in amplitude as they approach the tail. The speed of propagation of these waves is greater than the speed of forward travel (Frolich and Biewener, 1992; Gillis, 1997). The limbs are held against the side of the body, presumably for streamlining.

On land, salamanders may move by undulation (as in water), or they may walk, trot, or even jump. At slower speeds, salamanders generally walk with at least three feet in contact with the substrate at all times. Salamander walking is typically accompanied by standing waves of lateral bending in the trunk (Edwards, 1976). The timing of limb protraction and lateral bending is such that the length of each step is extended as the girdle of the protracting limb is rotated forward (Gray, 1968). As speeds increase, there is a shift to a trotting gait that leaves only two feet on the substrate at a given time (right front and left hind support alternating with left front and right hind support). At these higher speeds, stout bodied salamanders (e.g., *Ambystoma tigrinum*) continue to generate a standing wave with the nodes at approximately the point of the girdles (Edwards, 1976; Frolich and Biewener, 1992), and an increase in the amplitude of bending may be seen (Ashley-Ross, 1994). Attempts to locomote above some maximum speed often results in postural failure of the animal (they collapse onto the substrate). At this point they shift to undulation, although this is ineffective on the treadmills and trackways where it has been observed, and does not result in an increase in forward speed relative to trotting.

Elongate salamanders with functionally ineffectual limbs (e.g., the aquatic *Siren* and *Amphiuma*) will progress on land using lateral undulation. Here, the body is thrown into traveling waves that push against irregularities on the substrate, and the resultant force propels the body forward. Although this type of locomotion grossly resembles that of snakes, with complex waves forming along the body and all the points along the body following the same path during forward progression (Gans, 1985; Gillis, 1997; Gray and Lissman, 1950), it is unlikely that salamanders are capable of the level of fine motor control exhibited by snakes (Gans, 1985, 1986).

In addition to walking and undulation, some particularly specialized forms of locomotion, which are poorly studied, may be powered in whole or in part by axial musculature. For example, fossorial salaman-

ders (e.g., *Phaeognathus*) may construct burrows, presumably using both axial and appendicular musculature, or they may simply use preexisting tunnels. A type of pentapedal locomotion is known from *Hydromantes* in which the tip of the tail is anchored to the substrate off to one side of the trunk when climbing steep gradients (Stebbins and Cohen, 1995). In a most peculiar escape behavior, some *Hydromantes* will laterally flex the trunk to form a tight coil and then roll away down hill (García-París and Deban, 1995). Finally, some plethodontid salamanders are able to jump considerable distances by an as yet undescribed mechanism.

The anatomy of the salamander trunk

Salamanders have between 10 and 60 similarly shaped trunk vertebrae (Wake, 1966; Worthington and Wake, 1972). Most trunk vertebrae have short, y-shaped ribs. There is a well-developed atlas and the caudal vertebrae can be distinguished from the trunk vertebrae by the presence of hemal arches. Although regional differences are readily distinguished by the trained eye (Wake and Lawson, 1972; Worthington and Wake, 1972), the trunk vertebrae are much more uniform than those of a bird or mammal. The single sacral vertebra is usually somewhat stouter than surrounding vertebrae and has a relatively robust rib that articulates with the ilium of the pelvic girdle (Francis, 1934; Wake and Lawson, 1972; Worthington and Wake, 1972). A few caudosacral vertebrae that lack the hemal arches of caudal vertebrae are found caudal to the sacrum (Worthington and Wake, 1972).

The axial musculature of all craniates can be divided into two groups, a muscle mass dorsal to the horizontal septum, the epaxials, innervated by the dorsal rami of the spinal nerves, and a more ventral mass, the hypaxials, innervated by the ventral rami of the spinal nerves (see review by Fetcho, 1987). In salamanders, there are three epaxial muscles (Naylor, 1978). The *M. dorsalis trunci*, which is the largest in cross-sectional area, originates and inserts on transverse myosepta and bodies of the vertebrae. The *Mm. interspinalis* are a series of small muscles on the midline that originate

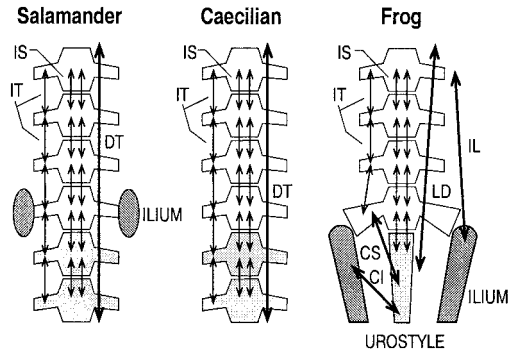


FIG. 1. A diagrammatic dorsal view of the epaxial musculature of the three living groups of lissamphibians. The epaxials are shown in relation to the vertebral column and the pelvic girdle when present. CI—*M. coccygeoiliacus*; CS—*M. coccygeosacralis*; DT—*M. dorsalis trunci*; IS—*M. interspinalis*; IL—*M. ilio-lumbaris*; IT—*Mm. intertransversarii*; LD—*M. longissimus dorsi*.

and insert on the spinous processes of the vertebrae. The *Mm. intertransversarii* are another series of small muscles lateral to the *Mm. interspinalis*; these originate and insert on the transverse processes of the vertebrae.

The hypaxial muscles fall into three categories, based on their relative position on the trunk (Fig. 2). The dorsal group is composed of two muscles, the *M. subvertebralis pars ventralis* that runs between the ventral surfaces of adjacent vertebral bodies, and the *M. subvertebralis pars transversalis* which runs between ribs (Francis, 1934; Naylor, 1978). In addition, there are three or four lateral hypaxial muscles (Naylor, 1978; Brainerd and Simons, 2000). The *M. obliquus externus* is the most superficial muscle of the lateral group. The *M. obliquus externus* is sometimes represented by two muscles, an outer *M. obliquus externus superficialis* and an inner *M. obliquus externus profundus*. When only a single layer of the external oblique is present, it is considered to be the profundus. The fiber direction of both the superficial and the deep layer is from craniodorsal to caudoventral. When present, the superficial layer is more vertically oriented than the deep layer. Medial to the *M. obliquus externus* are the *M. obliquus internus* and the *M. transversus*. In some species there is but a single muscle

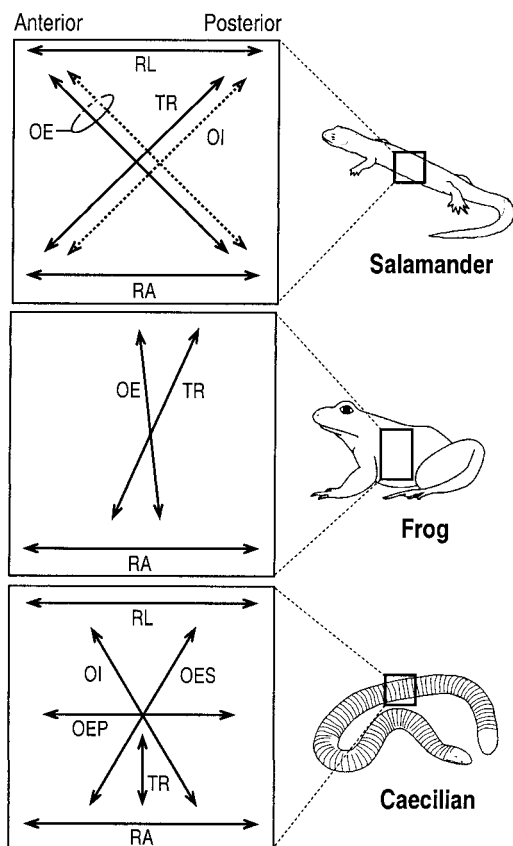


FIG. 2. A diagrammatic lateral view of the hypaxial musculature of the three living groups of lissamphibians. OE—*M. obliquus externus*; OEP—*M. obliquus externus profundus*; OES—*M. obliquus externus superficialis*; OI—*M. obliquus internus*; RA—*M. rectus abdominis*; RL—*M. rectus lateralis*; TR—*M. transversus*.

layer of uncertain homology; by convention this is called the *M. obliquus internus* (Brainerd and Simons, 2000). The fiber direction of both muscles is cranioventral to caudodorsal, with the *M. transversus* typically more vertically oriented. The sole muscle of the ventral muscle group is the *M. rectus abdominis*, which runs longitudinally along the ventral midline and is usually composed of distinct superficial and deep layers (Naylor, 1978).

Functional morphology of the salamander trunk

During swimming both the epaxial and hypaxial muscles bend the trunk to produce

traveling waves of lateral bending, which generate forward movement. Electromyograms (EMGs) of the epaxial musculature of the tiger salamander, *Ambystoma tigrinum*, from five points along the trunk, show sequential depolarization in the caudal direction at the same rate as wave propagation (Frolich and Biewener, 1992). Electromyographic data from the Pacific giant salamander, *Dicamptodon ensatus*, are consistent with the hypothesis that the lateral hypaxial musculature also contributes to lateral bending during swimming (Carrier, 1993).

In contrast to swimming, the axial musculature must play the dual roles of bending the trunk and resisting torsional forces during terrestrial quadrupedal locomotion (Fig. 3). During trotting in stout-bodied salamanders, the trunk assumes a standing wave with nodes at the level of the girdles (Roos, 1964; Edwards, 1976). In trotting tiger salamanders, as the standing wave moves to the left from the right side, the right-side epaxial muscles are synchronously active along the trunk (Frolich and Biewener, 1992). Thus epaxial EMGs from this species indicate a lateral bending function during both swimming and trotting. EMG data from the hypaxial muscles is only available from *Dicamptodon*. A comparison of hypaxial muscle activity during swimming vs. trotting reveals two qualitatively different patterns (Carrier, 1993). During swimming there is overlapping activity of all lateral hypaxial muscles, the two layers of the external oblique, the internal oblique, and the transversus. The overlapping activity, and the timing of muscle activity relative to lateral bending of the trunk, support a lateral bending function for the lateral hypaxial muscles during swimming. During trotting, however, the two layers of external oblique are active at the same time, followed by activity of the internal oblique and transversus. The four layers of lateral hypaxial muscles, by virtue of fiber orientation, are functionally divided into two pairs of muscles oriented so that one pair resists clockwise torsion and the other resists counter-clockwise torsion. The activity pattern of these muscles relative to foot support is consistent with a functional hypothesis of torsion

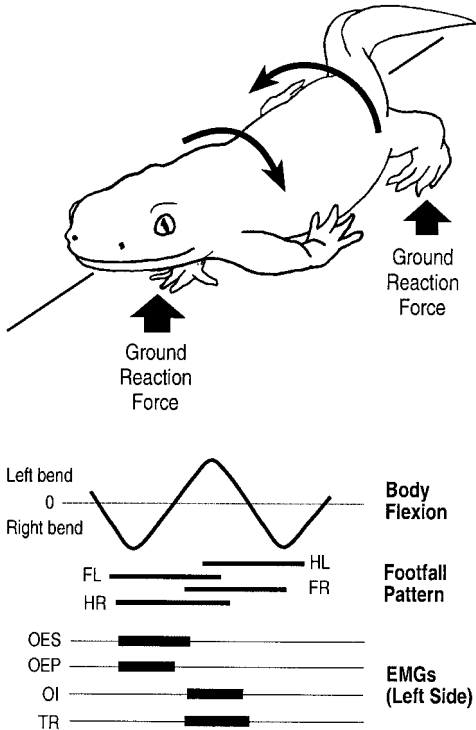


FIG. 3. Terrestrial locomotion in a stout-bodied salamander. The front left and rear right feet are off the ground, and the ground reaction forces are generating torsion as indicated by the curved arrows. Data from a representative stride show the pattern of body flexure and the footfalls. Electromyograms from the four layers of lateral hypaxial muscles on one side of the body indicate that they are resisting axial torsion. The two outer layers, the *M. obliquus externus superficialis* (OES) and *M. obliquus externus profundus* (OEP), are active on one side while presumably the *M. obliquus internus* (OI) and *M. transversus* (TR) are active on the other side. As the other pair of feet contact the ground this pattern reverses (modified from Carrier, 1993).

resistance. During the stance phase the outer two layers on one side are active with the inner two layers of the other side (Fig. 3) (Carrier, 1993). However, activity of the superficial and deep layers of the external oblique are also appropriately timed to contribute to lateral bending of the trunk. The bending function of the hypaxials was brought to light by denervation of the hypaxial layers of the five middle segments of a single side of the trunk in *Dicamptodon* (Ritter, 1998). Denervation of these muscles resulted in a significant reduction in bending of the trunk (Fig. 4).

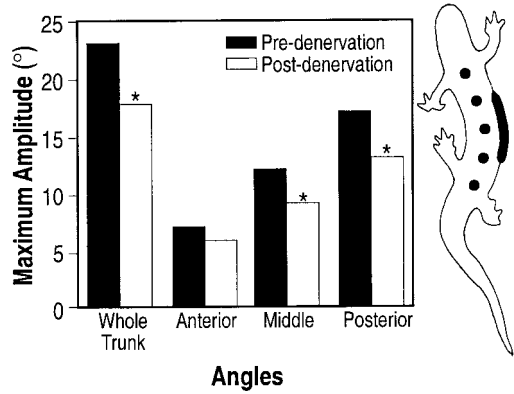


FIG. 4. Bar graph showing the reduction in bending of the body of *Dicamptodon* after hypaxial muscle denervation. Bending was measured as the angle between the points shown on the back of the salamander before and after denervation of hypaxial muscles in the region indicated by a heavy black line. The angle between the first, third, and fifth points is whole-trunk bending. The other bars represent the angles between the anterior, middle, and posterior three points respectively. * indicates paired t-test found significant differences pre- and post-denervation.

There are several interesting aspects of the functional morphology of the salamander trunk that have yet to be addressed. 1) Salamanders will move slowly, while submerged in the water, by walking along the bottom. This underwater walking differs from terrestrial walking in that the buoyancy of the animal will effectively remove gravitational effects, including long-axis torsion. Aquatic walking provides a promising natural experiment that may be employed to test the hypothesis that the hypaxial muscles resist torsion. 2) The long-held view that the trunk musculature, in concert with vertebral zygapophyses, maintains posture has never been tested. Specifically, it would be interesting to know the role of the epaxials in stiffening the trunk dorsoventrally. 3) A comparative functional study of jumping in salamanders and frogs would present an opportunity to quantify the functional consequences of behavioral and morphological specializations for saltation that have emerged during anuran evolution.

FROGS

In their most common form of aquatic locomotion, frogs use symmetrical or asym-

metrical motions of the hindlimbs to push themselves through the water. Frogs also use an alternating quadrupedal gait to crawl along the bottom or through vegetation. During swimming the forelimbs are typically retracted against the body during the power stroke; however, in some species (e.g., *Xenopus* and *Pipa*) the forelimbs are always held away from the body, and in *Hymenochirus* the front feet are webbed and appear to aid in propulsion. When jumping, the hindlimbs symmetrically propel the frog while the forelimbs are protracted anterior and laterally to help brace the trunk as the animal lands. Jumping ability varies greatly among living anurans (Marsh, 1994), and in fact some species jump only rarely, preferring to walk (Emerson, 1979).

In addition to the familiar jumping and walking, some more specialized locomotor modes are found among anurans. Burrowing ability has evolved many times. Most burrowing frogs (e.g., *Scaphiopus* and *Bufo*) construct burrows by digging with alternating movement of the hind limbs as the animal moves progressively backwards (Emerson, 1978; Summers and Delis, 1994). A few species (e.g., *Hemisus marmoratus* and *Leptodactylus bufonius*) burrow head first (Emerson, 1978). Many frogs are entirely arboreal, using expanded toe pads and exceptionally long limbs to climb. A subset of the arboreal frogs have adaptations for gliding flight such as webbing between extremely long digits (Emerson and Koehl, 1990).

The anatomy of the frog trunk

Adult anurans have a highly reduced vertebral column with only 6 to 9 pre-sacral vertebrae, one or two sacral vertebrae, and no ribs (Duellman and Trueb, 1986). These vertebrae are tightly joined allowing only minimal movement. The sacral vertebra is well developed with large, wing-like transverse processes to which the ilia are attached. The caudal vertebrae have been fused into a single rod-shaped skeletal element (the urostyle or coccyx) that lies between the ilia, in effect moving the tail internally (Gaupp, 1896). The spine has extremely reduced mobility at most points

with the exception of the iliosacral joint which usually allows considerable motion, and in most taxa the coccygeosacral joint is also mobile (Emerson, 1979).

Frogs have only three clearly defined hypaxial muscles (Duellman and Trueb, 1986; Fig. 2) including two very thin sheets that make up the body wall, an *M. obliquus externus* and an internal layer of uncertain homology that is usually referred to as the *M. transversus*. The longitudinally-fibered *M. rectus abdominis* originates on the pubis and runs anteriorly along the midline, splitting into distinct medial and lateral portions before inserting on the pectoral girdle and humerus respectively.

In contrast to the hypaxials, the epaxials are elaborate and well developed (Duellman and Trueb, 1986; Fig. 1). The *M. coccygeoiliacis* is a sheet of muscle that originates on the urostyle and inserts on the ilia. The *M. coccygeosacralis* originates on the urostyle and inserts on the sacral vertebra. The *M. interspinalis* and the *Mm. intertransversarii* are similar to those of salamanders. The *M. iliolumbaris* runs from the ilia, across the wings of the sacral vertebra, and inserts onto the presacral vertebrae (Emerson, 1979). The *M. longissimus dorsi* runs the length of the back, originating on the vertebrae and the fascia of the trunk and inserting on the urostyle.

Functional morphology of the frog trunk

Among frogs, the role of axial musculature during locomotion has received relatively little attention, both because of the short, stiff vertebral column and the distractingly obvious appendicular contribution to jumping. However, functional studies by Emerson and her colleagues (Emerson, 1978, 1979; Emerson and Koehl, 1990) and the recent functional analysis of Jenkins and Shubin (1998), reveal that the trunk musculature plays an integral role in all modes of frog locomotion (see below).

In at least some frogs, such as members of the genus *Rana*, the epaxial muscles play a pivotal role in saltation. A frog at rest will sit with its vertebral column nearly parallel to the ground. As the frog starts to jump it raises the anterior half of the trunk, putting the vertebral column at a more acute angle

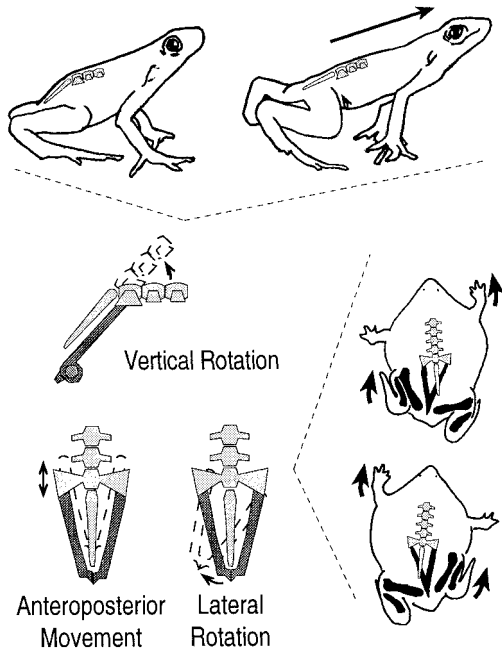


FIG. 5. The movements of the anuran pelvic girdle during jumping, walking, and swimming. The upper diagram illustrates vertical rotation of the vertebral column relative to the pelvic girdle (dark shading) and urostyle during jumping. The lower right diagram illustrates lateral rotation of the pelvic girdle relative to the vertebral column and urostyle during walking. The anterior-posterior movements seen in the lower left diagram are representative of movements during swimming (modified from Emerson, 1979; Jenkins and Shubin, 1998).

to the substrate (Fig. 5). This re-orientation of the body axis relative to the substrate results from an extension of the iliosacral joint, and is effected by the epaxial muscles spanning this joint, as well as the coccygeal muscles (Fig. 1). The action of these muscles, as well as the coccygeoiliacis, brings the ilia and urostyle into the same plane with the vertebral column (Jenkins and Shubin, 1998; Fig. 5). In this orientation the force generated by the leg muscles passes more nearly through the center of mass of the frog.

In addition to the dorso-ventral flexion seen during saltation, the sacroiliac joint often allows varying degrees of lateral movement (Emerson, 1979). In many walking frogs, the pelvis swings to the left or right side while the hind limb on that side of the body is in the swing phase (Fig. 5). This

has the effect of moving the femur farther forward than would be possible with an akinetic pelvis thereby increasing stride length (Emerson, 1979). This side to side movement is likely achieved by unilateral contraction of the iliolumbaris muscles. In some frogs, stride length is further increased by symmetrical forward movement of the entire pelvic girdle relative to the vertebral column. Similar antero-posterior pelvic movements have been observed in the aquatic frog *Xenopus* during swimming (Palmer, 1960).

The role of axial musculature in frog locomotion still presents several interesting problems. 1) Though we have a good grasp of the functional morphology of jumping, other modes, most notably swimming and burrowing, are still poorly understood. 2) The only axial musculature mentioned so far has been epaxials; the hypaxial muscles are greatly reduced in thickness relative to those of salamanders and are thought to play no role in locomotion. This functional hypothesis has yet to be tested, but if supported would indicate an important evolutionary shift in the functional role of trunk muscles. 3) The specific hypotheses regarding the function of the ilio-sacral joint during jumping, walking, climbing, burrowing, and swimming (Emerson, 1979) should be tested across a wide variety of frog taxa, with an eye towards finding functional intermediates and deviations from the diversity that has already been described.

CAECILIANS

Caecilians must power all locomotion with axial musculature as they are entirely limbless. Most caecilians are terrestrial burrowers, either constructing their own tunnels or living in the litter of the forest floor (Taylor, 1968; Renous and Gasc, 1989a). However, some species are semi-aquatic, and one lineage of South American caecilians is completely aquatic (Taylor, 1968; Wilkinson and Nussbaum, 1999). In water, caecilians generally move by swimming undulation, generating traveling waves down their bodies. The nature of these waves and how they vary with speed or among species has not been described. The behavior is presumably similar to the anguilliform swim-

ming of eels and elongate salamanders. When moving through debris or vegetation under water, caecilians also employ lateral undulation.

While burrowing, caecilians employ concertina locomotion, lateral undulation, and vermiform locomotion (Gaymer, 1971; Gans, 1973; Renous and Gasc, 1993; Summers and O'Reilly, 1997). In the experimental arena, concertina is most easily elicited by placing an individual in a smooth, straight-sided channel or tube (Gaymer, 1971; Renous and Gasc, 1993). The lack of anteriorly directed push points makes lateral undulation impossible, and the animal will throw its body into S-shaped curves that press against opposite sides of the channel. The body exerts forces normal to the direction of travel that result in a static friction force against which the rest of the body can be pushed or pulled (Gray, 1946). Some caecilians have the ability to move the vertebral column and associated musculature independently of the body wall; this is referred to as "internal concertina" or "vermiform locomotion." The independence of the vertebral column from the body wall makes it possible for the animal to change its total length and average diameter (Gaymer, 1971; Gans, 1973).

Anatomy of the caecilian trunk

Relative to salamanders and frogs, the caecilian vertebral column displays very little regional specialization and there is no trace of girdles or limbs (Taylor, 1977; Wake, 1980; Renous and Gasc, 1986a, b; 1989a, b). Among caecilians, there is a great deal of variation in both body proportions and the number and size of vertebrae. Some genera (*e.g.*, *Oscacaecilia*) are extremely elongate with over 250 vertebrae, while others (*e.g.*, *Epicrionops*) have stouter body proportions and as few as 70 vertebrae (Taylor, 1968; Renous and Gasc, 1986b, 1989a, b).

The epaxial muscles are similar to those of salamanders and consist of the *M. dorsalis trunci* and *M. interspinalis* that envelop the dorsal side of the vertebral column (Naylor and Nussbaum, 1980; Nussbaum and Naylor, 1982; Fig. 1). The hypaxial muscle group is quite complex. Two small

muscles are closely associated with the vertebral column, with one muscle running between the epaxial muscle mass and the hypaxial muscles of the body wall (Fig. 2). The *M. subvertebralis* and the basapophyseal muscles encase the ventral side of the vertebral column. The *M. subvertebralis pars ventralis* originates on the mid-ventral surface of the vertebral column and inserts on the lateral hypaxial body wall musculature (Naylor and Nussbaum, 1980). The body wall musculature consists of three longitudinal muscles that form a continuous layer around the body (Naylor and Nussbaum, 1980). The *M. rectus abdominis* runs along the ventral midline. The *M. obliquus externus profundus* makes up the longitudinal component of the lateral body wall and the *M. rectus lateralis* lies dorsal to all the lateral body wall musculature. In addition, three vertically oriented muscles contribute to the body wall (Naylor and Nussbaum, 1980). The *M. obliquus externus superficialis* has a craniodorsal to caudoventral orientation, while fibers of the *M. obliquus internus* are oriented at 90 degrees to the external oblique. Both muscles insert directly into tendinous fibers that are imbedded in the body wall and organized in a crossed helical array that surrounds the entire trunk (O'Reilly *et al.*, 1997). The final body wall muscle is the *M. transversus*, which is vertically oriented and runs from the insertion of the ventral part of the subvertebralis to a tendinous sheet that holds the viscera in a transverse sling (Naylor and Nussbaum, 1980).

The functional morphology of the caecilian trunk

A caecilian is essentially composed of a vertebral column and associated muscles that, along with the viscera, are wrapped within a tube of several layers of hypaxial musculature (Gaymer, 1971; Naylor and Nussbaum, 1980; Nussbaum and Naylor, 1982; von Schnurbein, 1935). The vertebral muscles and body wall muscles form separate functional units that are linked together by the ventral portion of the subvertebralis. The vertebral musculature is composed of both epaxial and hypaxial muscles and functions to bend or stabilize regions

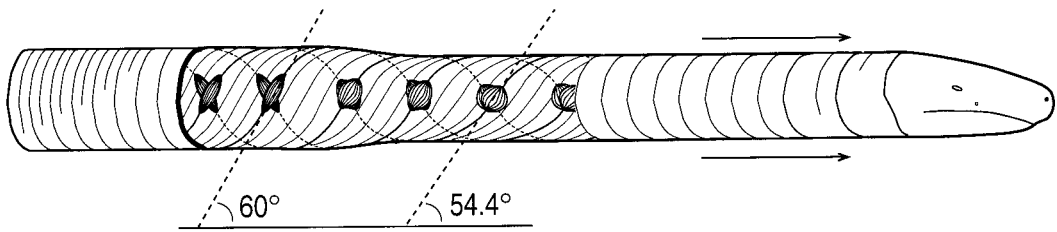


FIG. 6. The hydrostatic skeleton of a caecilian. The posterior, fatter portion of the animal is illustrated at rest. The body pressure is low and the fiber angles are near 60° . The anterior, thinner part of the animal is illustrated during contraction of the superficial external oblique and internal oblique which drives the head forward as tension causes the fiber angle in the *stratum compactum* to shift towards 54.4° (modified from O'Reilly, Ritter and Carrier, 1997).

of the vertebral column. Thus, the vertebral muscles are almost certainly involved in forming traveling waves during swimming, and standing waves during both lateral undulation and vermiform locomotion.

The body wall musculature is entirely made up of hypaxial muscles and is associated with a complex of tendons and tendinous sheets (von Schnurbein, 1935) which play multiple roles during different modes of locomotion. An anesthetized caecilian is completely flaccid, suggesting that the rigid posture seen in conscious individuals is generated by hydrostatic pressure in the body cavity (Carrier and Wake, 1995). In fact, not only is hydrostatic pressure important in maintaining posture, but it also plays a key role in generating propulsive forces. While burrowing using vermiform locomotion, the forces generated by a caecilian are far in excess of what would be predicted by the cross sectional area of the muscles in the transverse plane (O'Reilly *et al.*, 1997). This apparent "super strength" is achieved by a contribution to forward force by vertically oriented muscles in the body wall. The superficial external oblique and internal oblique insert into fibrous tendons that become the multi-layered *stratum compactum* of the dermis. The angle between these fibers is approximately 60 degrees when the animal has thrown the vertebral column into S-curves within the body wall. When the transversus has pressurized the visceral cavity, contracting the internal oblique and superficial external oblique generates tension in the connective tissue helix, which tends to elongate the active area of the body wall until the angle be-

tween the alternating layers of the dermis is more nearly 54.4 degrees (Kier and Smith, 1985; Fig. 6). As the body wall extends forward, it moves anteriorly at a faster pace than the vertebral column, and body diameter in the region of elongation decreases (Summers and O'Reilly, 1997). In this way, forces generated by the vertically oriented hypaxial muscles are translated into longitudinal forces (O'Reilly *et al.*, 1997).

During lateral undulation and swimming undulation, the outer body wall of caecilians moves in synchrony with the vertebral column (Summers and O'Reilly, 1997). Bends in the body wall are most likely created by contraction of the longitudinally oriented hypaxial muscles (lateral rectus, profundus portion of the external oblique and abdominal rectus), as well as the dorsalis trunci. Contraction of the ventral portion of the subvertebralis may play a role in keeping the vertebral column bending at the same rate as the body wall.

Several additional aspects of caecilian locomotion remain open to question. 1) It seems probable that effective vermiform locomotion evolved within the extant caecilians. The presence or absence of the functional and morphological features that make this mode of locomotion possible, such as a thick *stratum compactum* and slack spinal nerves, has not been determined in basal taxa such as *Epicrionops* and *Rhinatrema*. Among more nested gymnophiones, the aquatic members of the Typhlonectidae appear to have lost the ability to perform vermiform locomotion (Summers and O'Reilly, 1997). Is this accompanied by morphological specializations of the mus-

culature for lateral and swimming undulation? 3) A number of caecilians are extremely thin (*e.g.*, *Boulengerula* over 40 cm long may only be 5mm in diameter). There are no data on the functional consequences of such a narrow body plan, although it would certainly seem to preclude the use of vermiform locomotion.

THE EVOLUTION OF TRUNK MUSCLE FUNCTION IN AMPHIBIANS

Any attempt to discuss the evolution of trunk characteristics within Lissamphibia runs into at least two potential difficulties. The relationships between the three extant orders are entirely unresolved; all three possible arrangements of the three taxa have been advanced (Trueb and Cloutier, 1991b). This is in part due to the very long branch lengths of the three clades and the extreme morphological specializations seen in two of the three groups. The other potential problem is that the trunks of the earliest tetrapods did not look very much like those of any of the modern lissamphibian groups. They were heavy boned, with large ribs and many were of quite large size (Carroll, 1988; Jarvik, 1980). Bearing in mind these two issues, we propose that it is still possible to plausibly reconstruct the configuration of the trunk muscles in the ancestor of Lissamphibia.

The scant fossil record suggests that the common ancestor of living amphibians had a salamander-like body plan (Carroll, 1997; Wake, 1997). The most commonly proposed sister taxon to the lissamphibians is a paraphyletic group, the "dissorophids" (*sensu* Bolt, 1991). These amphibians were more like modern salamanders than basal tetrapods in body form. Within the dissorophids, the possibly paedomorphic "branchiosaurids" have been proposed as the immediate sister taxon to the extant lissamphibians (Boy, 1987). Branchiosaurs are remarkably similar to modern salamanders in their proportions and morphology. The earliest known anuran ancestor (*Triadobatrachus*) had 14 presacral vertebrae and numerous caudal vertebrae and represents an intermediate trunk design between those of living salamanders and frogs (Rage and Roček, 1989). Similarly, a recently described

fossil caecilian with an appendicular skeleton exhibits an intermediate form between the salamander body plan and that of the limbless, and tailless caecilians (Jenkins and Walsh, 1993). From the available fossil data and the assumption that Lissamphibia is a monophyletic group derived from within the "dissorophids," we conclude that the ancestral lissamphibian most likely had a salamander-like body form.

The plesiomorphic arrangement of the trunk muscles of salamanders can be inferred from the living sister taxa to the tetrapods. The Dipnoi (lungfish) represent a particularly relevant outgroup as they, like Lissamphibia, are generally paedomorphic (Bemis, 1984). There are five hypaxial muscles in both the African (*Protopterus*) and South American (*Lepidosiren*) lungfishes (Maurer, 1912). The hypaxials consist of superficial and deep external obliques, an internal oblique, and two distinct layers of the rectus abdominis. The epaxials are a single, large mass, the *dorsalis trunci*. The Australian lungfish (*Neoceratodus*) is much the same except for having a single external oblique (Maurer, 1912). Thus, the arrangement of trunk muscles in lungfishes is extremely similar to the arrangement of muscles seen in salamanders, the most notable difference being the lack of subvertebralis, interspinalis or intertransversarius muscles.

Relative to the salamander-like arrangement of trunk muscles in their common ancestor, frogs and caecilians have taken very different paths towards specialization of the trunk. Frogs have radically truncated vertebral columns, relatively large hindlimbs, and a well-developed array of epaxial musculature. Lateral bending of the trunk is absent during all forms of adult frog locomotion and the epaxial muscles have become specialized instead to both sagittally extend and stabilize the ilio-sacral and ilio-coccygeal joints, the only flexible points in the anuran vertebral column. The hypaxial muscles play no apparent role in anuran locomotion. Thus, the functional role of both groups of trunk muscles exhibits substantial differentiation relative to the common ancestor of lissamphibians (Fig. 7).

In contrast to frogs, caecilians have a

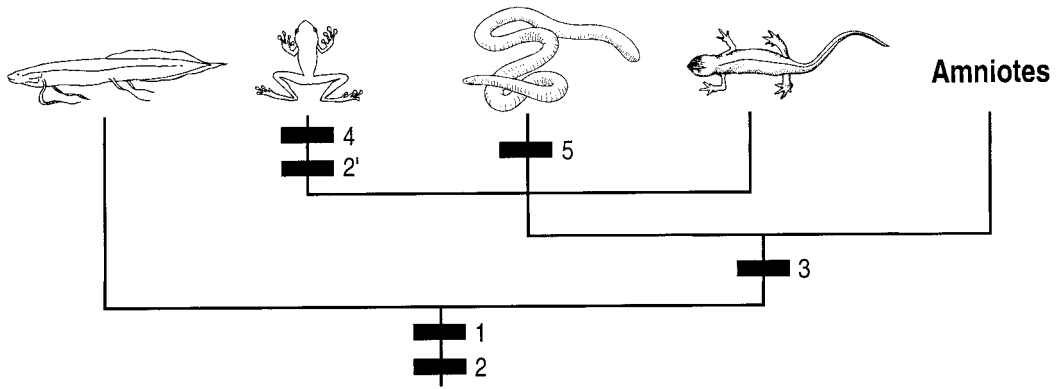


FIG. 7. A cladogram with hypothesized functional transitions for the axial musculature in Lissamphibia (Anura, Gymnophiona and Caudata) and two sister taxa (Dipnoi and Amniota). 1—epaxial muscles used for lateral bending; 2—hypaxial muscles used for lateral bending; 3—axial musculature resists torsional forces; 4—epaxial muscles used for jumping; 5—hypaxial muscles power hydrostatic skeleton. ' indicates character loss.

radically elongated vertebral column, no limbs or girdles, and relatively elaborate hypaxial musculature. The muscles of the trunk have apparently retained all of the functional roles seen in the trunk muscles of salamanders. Contraction of both epaxial and hypaxial muscle layers plays a critical role in all caecilian locomotor modes, both muscle groups retaining their role as trunk-bending muscles. Although the limbs are no longer present, caecilians still generate ground reaction forces, and the muscles of the trunk must stabilize the trunk during locomotion. In addition to retaining the ancestral roles, the trunk muscles must operate the hydrostatic skeleton which is used for posture and to generate forward forces during vermiform locomotion (Fig. 7).

Recent studies of both the functional anatomy of living amphibians, and descriptions of new fossil material have led to a more robust picture of amphibian trunk evolution. The specialization of both frog and caecilian trunk anatomy is associated with evolutionary changes in both locomotor behavior and the functional role of trunk muscles in locomotion (Fig. 7). This review of the available data reveals unambiguous cases of muscle functions being lost (*e.g.*, the epaxial and hypaxial muscles no longer bending the vertebral column in adult frogs) and being added (*e.g.*, the emergence of the hydrostatic skeleton of caecilians). However, there are no clear cas-

es of muscle function shifting from one muscle group to another. The exact roles of the trunk muscles during some forms of locomotion are still poorly understood, while their roles in several more specialized modes of locomotion (like frog gliding and salamander jumping) have yet to be approached in any experimental studies. Lastly, the functional studies to date have focused on only a handful of species, and more comparative studies are needed to determine how widely the patterns described thus far can be applied.

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