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AUTHORS: Julia L. Molnar, Rui Diogo, John R. Hutchinson, Stephanie E. Pierce

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Evolution of hindlimb muscle anatomy across the tetrapod water-to-land transition, including comparisons with forelimb anatomy

Julia L. Molnar[1]*, Rui Diogo[2], John R. Hutchinson[3] and Stephanie E. Pierce[4]

1. New York Institute of Technology College of Osteopathic Medicine, Department of Anatomy, Northern Boulevard, Old Westbury, NY, USA
2. Howard University College of Medicine, Department of Anatomy, 520 W St. NW, Numa Adams Building, Washington DC 20059, USA
3. Royal Veterinary College, Structure and Motion Lab, Hawkshead Lane, Hatfield, Hertfordshire, AL9 7TA, UK
4. Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA

* Corresponding author: Julia L. Molnar, New York Institute of Technology College of Osteopathic Medicine, Rockefeller Building room 314D, Northern Boulevard, Old Westbury, NY 516-686-3965, jedwar10@nyit.edu

ABSTRACT

Tetrapod limbs are a key innovation implicated in the evolutionary success of the clade. Although musculoskeletal evolution of the pectoral appendage across the fins-to-limbs transition is fairly well documented, that of the pelvic appendage is much less so. The skeletal elements of the pelvic appendage in some tetrapodomorph fish and the earliest tetrapods are relatively smaller and/or qualitatively less similar to those of crown tetrapods than those of the pectoral appendage. However, comparative and developmental works have suggested that the musculature of the tetrapod forelimb and hindlimb was initially very similar, constituting a "similarity bottleneck" at the fins-to-limbs transition. Here we used extant phylogenetic bracketing and phylogenetic character optimization to reconstruct pelvic appendicular muscle anatomy in several key taxa spanning the fins-to-limbs and water-to-land transitions. Our results support the hypothesis that transformation of the pelvic appendages from fin-like to limb-like lagged behind that of the pectoral appendages. Compared to similar reconstructions of the pectoral appendages, the pelvic appendages of the earliest tetrapods had fewer muscles, particularly in the distal limb (shank). In addition, our results suggest that the first tetrapods had a greater number of muscle-muscle topological correspondences between the pectoral and pelvic appendages than tetrapodomorph fish had. However, ancestral crown-group tetrapods appear to have had an even greater number of similar muscles (both in terms of number and as a percentage of the total number of muscles), indicating that the main topological similarity bottleneck between the paired appendages may have occurred at the origin of the tetrapod crown group.

Keywords: Sarcopterygii, stem tetrapods, fins-to-limbs, Acanthostega, Eusthenopteron, Pederpes, pelvic appendage, locomotion

INTRODUCTION

The origin of tetrapod limbs from fish fins was not simply a series of stepwise changes from fish-like to tetrapod-like morphology. Some early tetrapods and their close relatives displayed distinctive characteristics or groups of characteristics unknown in extant tetrapods. For example, the earliest known tetrapod hindlimbs (belonging to the Devonian tetrapods *Ichthyostega* and *Acanthostega*) had more than five digits (Coates and Clack 1990). *Ichthyostega* had a unique combination of postcranial characteristics: a derived forelimb with an anteroventrally positioned radial articulation and a bifid olecranon process, a paddle-like hindlimb, and a vertebral column with an almost mammal-like degree of regionalization (Ahlberg et al. 2005; Pierce et al. 2012, 2013a, b). The balance of evidence from fossil, evo-devo, and functional studies suggests that the transformation of the pelvic appendage lagged behind that of the pectoral appendage (Andrews and Westoll 1970; Edwards 1977; Boisvert 2005; Cole et al. 2011; Pierce et al. 2013b; Shubin et al. 2014). Several studies have also suggested divergent functions for the forelimb and the hindlimb during locomotion (e.g., Gregory 1928; Ahlberg et al. 2005; Boisvert 2005; Pierce et al. 2012, 2013b).

Although the earliest tetrapods were almost certainly mainly aquatic (Coates and Clack 1995), limbs were a key innovation that allowed tetrapods to eventually walk and live on land. It has been hypothesized that the first limbs helped their owners to push through vegetation, walk underwater, or dig underwater burrows and were later “exapted” for terrestrial locomotion (Coates and Clack 1995), but the ancestral musculoskeletal configuration of the limbs and the sequence of changes that led to modern tetrapod limbs is unknown. Recently, we investigated the origin and evolution of the tetrapod forelimb by reconstructing pectoral appendicular musculoskeletal anatomy in tetrapodomorph fish and early tetrapods spanning the fins-to-limbs and associated water-to-land transitions (Molnar et al. 2017a). The study inferred a sequence of muscle differentiation in the tetrapod lineage based on fossil morphology, muscle homology between extant sarcopterygian (fish and tetrapod) groups, and phylogenetic relationships. This was the first such work to trace muscle evolution all the way from the last common ancestor of extant sarcopterygian fish to crown tetrapods.

We found that many tetrapod shoulder muscles probably were already present in tetrapodomorph fish, whereas most of the more distal appendicular muscles either arose later from largely undifferentiated dorsal and ventral muscle masses or did not leave clear correlates of attachment in these taxa (Molnar et al. 2017a). Our results were largely congruent with previous muscle reconstructions such as that of the porolepiform *Glyptolepis* (Ahlberg 1989)*,* the stem tetrapod *Ossinodus* (Bishop 2014), and the early amphibian *Eryops* (Miner 1925). A reconstruction of the tetrapodomorph fish *Eusthenopteron* with tetrapod-like muscles (Andrews and Westoll 1970) was not supported: the osteological correlates of many tetrapod muscles identified in this fish, such as the origin of *coracobrachialis* on the scapulocoracoid, were not found in any close relatives and could not be traced to the last common ancestor of tetrapods. More broadly, our study provided an evidence-based framework for muscle reconstruction in stem tetrapods and laid the groundwork for investigations of forelimb function in the earliest tetrapods.

However, questions regarding the evolution of tetrapod hindlimb musculoskeletal anatomy remain open. For example, was there a point (or multiple points) in tetrapodomorph evolution when at least some parts of the pectoral and pelvic appendages, in particular the zeugopodia and autopodia, were very similar to each other, as suggested by Coates and Cohn (1998), Diogo and Molnar (2014) and Diogo et al. (2016)? Or, were the tetrapod forelimb and hindlimb initially markedly different from each other (Andrews and Westoll 1970; Boisvert 2005; Pierce et al. 2013b)? The skeletal structures of the pelvic fin and girdle in most tetrapodomorph fish such as *Eusthenopteron* and *Panderichthys* are much smaller than those of the pectoral fin and girdle, and the hindlimb elements in *Acanthostega* and *Ichthyostega* are flatter and more paddle-like than the forelimb, with less prominent processes for muscle attachment (Andrews and Westoll 1970; Clack and Coates 1995; Coates 1996; Boisvert 2005; Pierce et al. 2012, 2013b). These osteological features may support the inference that tetrapod hindlimb musculoskeletal anatomy lagged behind that of the forelimb. Yet, other explanations might also be viable. For instance, the pelvic fin muscles might have been smaller and therefore less likely to leave obvious osteological correlates. Alternatively, *Panderichthys* and *Eusthenopteron* might not be representative of the fish that gave rise to tetrapods in terms of relative size and muscle specializations. In fact, the pelvic girdle of the tetrapodomorph fish *Tiktaalik* is much larger than that of *Panderichthys* or *Eusthenopteron*, although the overall morphology is similar (Shubin et al. 2014).

Here we reconstruct the muscle anatomy of the pelvic appendage across the fins-to-limbs transition and discuss the idea of similarity between the paired appendages during tetrapod evolution. Coates and Cohn (1998) and Diogo and Molnar (2014) predicted the existence of a "similarity bottleneck" during the fins-to-limbs transition, at which point the forelimb and hindlimb had a greater number and/or percentage of topologically similar muscles than at any other point in vertebrate evolutionary history. This prediction followed the hypothesis that the greater number of similarities between the fore and hindlimbs of modern tetrapods resulted from independent recruitment of similar gene networks during the origin of tetrapod limbs (Willmer 2003; Diogo et al. 2013). Specifically, Diogo and Molnar (2014) hypothesized that in early tetrapods the muscles of the zeugopodia (forearm and shank) and autopodia (manus and pes) were almost identical to each other in terms of number and configuration of muscles, while the muscles of the phylogenetically older structures (stylopodia – arm and thigh – and, particularly, the girdles) remained markedly different, as they often are in fishes. Comparison of muscle reconstructions in the pelvic (this study) and pectoral appendage (Molnar et al. 2017a) of early tetrapods and their close relatives can therefore provide further information about how similar the two pairs of limbs initially were (or were not) during the fins-to-limbs transitions in terms of both functional morphology and topological organization.

MATERIALS AND METHODS

We reconstructed pelvic appendicular muscle anatomy in several key taxa spanning the water-to-land and fins-to-limbs transitions using extant phylogenetic bracketing (EPB); an application of outgroup analysis in phylogenetics (Witmer 1995). The EPB infers the presence or absence of soft tissues in extinct animals based on their presence or absence in closely related extant taxa – in this case coelacanths, lungfish, amphibians, and reptiles – and their presumed causal association with osteological features such as scars and tuberosities (Witmer 1995). We used the EPB in combination with comparative methods to infer a sequence of muscle differentiation between the last common ancestor (LCA) of crown-group sarcopterygians and the LCA of crown-group tetrapods. Next, we reconstructed the pelvic fin muscles of *Eusthenopteron,* a tetrapodomorph fish closely related to tetrapods, and the hindlimb muscles of the Devonian stem-tetrapod *Acanthostega,* one of the earliest tetrapods known from extensive postcranial remains. Finally, we compared these results with those for the pectoral appendage (Molnar et al. 2017a).

Methods of muscle reconstruction followed Molnar et al. (2017a); readers should refer to this publication for a detailed description. Briefly, homologous osteological correlates were conjectured based on hypotheses of muscle homology between extant sarcopterygian fish and tetrapods proposed in Diogo et al. (2016) (Fig. 1, Table 1). Examples of these osteological correlates are shown in Figs. 2-5. Next, using the literature and direct examination of specimens, the character state of each correlate in seven extant and 20 fossil sarcopterygian fish and tetrapods (Table 2) was recorded in a data matrix (Tables S1-3). Finally, parsimony-based character mapping (e.g., Hutchinson 2001) was performed in the software Mesquite (Maddison and Maddison 2018) using a phylogeny based on Ruta et al. (2003) and Ruta (2011) to infer the most likely character state for each node in the phylogeny, thereby proposing a sequence of changes of linked osteological and myological character states via the EPB method (analysis using maximum likelihood yielded the same results). An alternative phylogeny by Pardo et al. (2017) was also tested (Table S5).

The extant taxa included in the study were chosen as representative examples of the two closest sister groups of tetrapods (Coelacantha and Dipnoi) and the two major clades of extant tetrapods (Amniota and Lissamphibia) (Table 2). Particular species were chosen because they are well-described and show a generalized morphology for their clade. We identified fossil taxa to include in our analysis based on phylogenetic position and the availability of detailed descriptions, illustrations, photographs, and/or specimens or casts for direct observation (Table 2). A representative selection of tetrapodomorph fish and stem tetrapods for which sufficient appendage information was available was included because these groups are closest to the fins-to-limbs (and water–land) transition. We also included several non-tetrapodomorph sarcopterygians from the lineages leading to lungfish and coelacanths to help distinguish which characteristics of extant lobe-finned fishes are common to all sarcopterygians, as well as several stem amphibians and stem reptiles.

RESULTS

Based on the order in which their correlates appear in the phylogeny, we inferred an evolutionary sequence of differentiation of the pelvic appendicular muscles at specific nodes (Fig. 6). In figure 6, colored horizontal bars indicate muscle masses, and bifurcations indicate that the mass should be considered as separate muscles at that node and crownward. The branching points were inferred based on both homology hypotheses and the distribution of osteological correlates, and the logic for their placement is explained in the following subsections. At node 1 (Tetrapodomorpha), the posteroventral process of the pelvis (PVP, Fig. 4B) or the transverse line of the ilium (TLI, Fig. 5A) was present, marking the origins of the *tenuissimus* (iliofibularis) and/or *iliofemoralis*. Considering that the homologue of the latter muscle was hypothetically present in the LCA of crown-group sarcopterygians, we consider these osteological features to most likely indicate the presence of the *iliofemoralis*. At node 2 (Elpistostegalia), the intertrochanteric fossa (ITF, Fig. 4D) appeared on the femur, marking the insertions of *puboischiofemoralis externus,* possibly combined with the *adductor femoris*, and *puboischiofemoralis internus.* Node 3 (Tetrapoda) marks the first appearance of many osteological correlates of muscle attachment: on the pelvis the mesial iliac ridge (MRPel, Fig. 5B) marks the posterior extent of the origin of *puboischiofemoralis internus*; on the femur the adductor crest (AdC, Fig. 5D) marks the insertion of *adductor femoris*; on the tibia the cnemial crest (CC, Fig. 5E) marks the insertion of *quadratus femoris* (triceps femoris; includes *extensor* *iliotibialis, iliofemoralis,* and, in amniotes, *ambiens*) and a system of ridges or a crest on the ventral aspect of the tibia (VCT, Fig. 5F) marks the insertion of *gracilis* (puboischiotibialis) and/or *ischioflexorius* (biceps femoris/flexor tibialis); and on the posterior edge of the fibula the ventral fibular ridge (VRFib, Fig. 5F) marks the origin of the crural head of the long digital flexors (*flexor digitorum communis, flexor accessorius lateralis* and *medialis*). At node 4 (post-Devonian tetrapods), muscle scars appeared on the fibular condyle of the femur and/or the adjacent intercondylar fossa (scars, Fig. 5C), marking the origin of *extensor digitorum longus,* and the fibular fossa (FF, Fig. 5D) marks the origin of *flexor digitorum communis*. At node 5 (*Crassigyrinus* and more crownward tetrapods), ridges appeared on the opposing aspects of the tibia and fibula, marking the attachments of *interosseous cruris*, and a distinct muscle scar appeared on the extensor aspect of the proximal fibula, marking the insertion of *tenuissimus*. Finally, at node 6 (crown Tetrapoda), distinct groups of scars appeared on the lateral aspect of the ilium just above the acetabulum marking the origins of *extensor iliotibialis* and *tenuissimus*; scars appeared on the fibular epicondyle marking the origin of *extensor cruris et tarsi fibularis* (fibularis longus et brevis)*;* a distinct scar appeared on the dorsal aspect of the femoral head, marking the insertion of *ischiotrochantericus;* and the ventral ridge of the tibia appeared, marking the origins of *extensor cruris tibialis* and *extensor tarsi tibialis* (tibialis anterior).

The alternative phylogeny (Pardo et al. 2017) produced similar results (compare Tables S4 and S5). However, there are a few differences that would affect the reconstruction of muscles in post-Devonian tetrapods. Several muscle attachments that had been mapped to node 6 were instead mapped to the node including *Archeria* and more crownward tetrapods (between nodes 5 and 6): the pelvic attachments of *tenuissimus* and *ischiotrochantericus* and the femoral attachment of *ischiotrochantericus*. Conversely, two attachments that had been mapped to more basal nodes moved crownward: the attachment of *extensor digitorum longus* on the femur moved from node 4 to node 6, and the attachment of *iliofemoralis* on the femur moved from node 6 to a clade within crown Tetrapoda (Squamata).

Superficial dorsal musculature

In the LCA of crown-group sarcopterygians, the bulk of the superficial dorsal musculature of the pelvic appendage was probably partially divided proximodistally by tendinous intersections at the level of each axial mesomere, as is the case in the pelvic fin of *Neoceratodus* and *Protopterus* and the pectoral fin of *Latimeria* (Braus 1900; Millot and Anthony 1958; King and Hale 2014; Diogo et al. 2016). The LCA of crown-group sarcopterygians also probably had a slender muscle derived from the superficial dorsal muscle mass running along the postaxial edge of the fin that was not divided proximodistally (*pterygialis caudalis*) (Table 1). However, few pelvic fins are clearly preserved in stem sarcopterygians, so little can be said confidently about their musculature. Not until the origin of tetrapods do characters appear that indicate complete division of the superficial dorsal musculature into individual muscles, as opposed to partial separation via tendinous intersections. A cnemial crest (insertion of the *quadratus femoris* group in crown tetrapods) is present on almost all tetrapod tibiae we examined (Table S3), indicating that the proximal portion of the superficial dorsal musculature inserted onto the proximal aspect of the crus in these taxa rather than continuing into the distal portion of the limb. In several stem tetrapods, muscle scars are present on the extensor side of the proximal fibula: “striae” in *Crassigyrinus* (Panchen and Smithson 1990 p. 39) and “a prominent roughened tubercle” in *Baphetes* (Milner and Lindsay 1998 p. 230). These scars probably mark the insertion of *iliofibularis;* a similar marking (“a rugosity at the anterolateral edge of the proximal half of the fibula”) was interpreted in this way in the seymoriamorph *Discosauriscus* (Klembara and Bartík 1999 p. 309). Therefore, the postaxial portion of the superficial dorsal musculature in these post-Devonian tetrapods was fully divided into proximal and distal portions (*iliofibularis* and *extensor cruris et tarsi fibularis,* respectively). In contrast, in the LCA of tetrapods the superficial dorsal musculature is reconstructed as consisting of several large, undifferentiated masses.

Deep dorsal musculature

The deep dorsal musculature of the pelvic appendage of the extant sarcopterygians *Latimeria* and *Neoceratodus* consists of two muscle groups: the more superficial *adductor profundus* and the deeper pronators. Because the *adductor profundus* and *pronator 1* each are hypothesized to be homologous with an individual tetrapod muscle (*puboischiofemoralis internus* and *iliofemoralis,* respectively (Table 1) (Diogo et al. 2016), the presence of osteological correlates for these muscles is interpreted here as a second line of evidence supporting their presence in stem sarcopterygian fish. Pronators 2-4 are hypothesized to be homologous with intrinsic muscles of the pes, so we did not attempt to trace their osteological correlates. In the fossil lungfishes *Griphognathus* and *Chirodipterus,* the posteroventral process of the pelvis was interpreted as the origin of *pronator 1* ("dorsolateral abductor-levator") by Young et al. (1989)*,* providing fossil evidence to support the hypothesis that this muscle was present plesiomorphically in lungfish. Therefore, the posteroventral process may be homologous with the transverse line of ilium beneath which the homologous muscle *iliofemoralis* is thought to have had its bony origin in stem tetrapods such as *Ichthyostega* (Jarvik 1996) and *Ossinodus* (Warren and Turner 2004), as well as most of the crown tetrapods we surveyed. In *Griphognathus* and *Chirodipterus,* "flat surfaces on the dorsal aspect of dorsomesial process" were identified as the origin of *adductor profundus/ puboischiofemoralis internus* ("dorsomesial adductor-levator") (Young et al. 1989), and a rounded vertical ridge on the medial aspect of the pelvis, present in all of the tetrapods we examined in which this region was preserved, was identified as the posterior extent of this muscle in the stem tetrapod *Acanthostega* (Coates 1996) and the crown tetrapods *Archeria* (Romer 1957), *Proterogyrinus* (Holmes 1984), and *Captorhinus* (Holmes 2003).

Superficial ventral musculature

Like its dorsal counterpart, the superficial ventral musculature of the pelvic appendage was probably partially divided proximodistally into multiple units, each spanning a single mesomere, with the exception of a single long muscle spanning multiple segments (in this case, *pterygialis cranialis* on the preaxial edge of the fin) (Diogo et al. 2016). Fossil evidence that the superficial ventral muscle mass was differentiated into individual muscles is scarce in non-tetrapod taxa. Among fossil tetrapods, the fibular fossa of the femur, a "deep, subcircular depression" "in front of the [fibular] condyle on the ventral surface," was interpreted as the origin of *flexor digitorum longus* in the stem amniote *Eoherpeton* (Smithson 1985 p. 373). Alternatively, this fossa has been suggested to have accommodated joint ligaments in, e.g., *Proterogyrinus* (Holmes 1984). The fibular fossa is also present in the stem tetrapods *Acanthostega* (Coates 1996) (FF, Fig. 4D)*, Tulerpeton* (Lebedev and Coates 1995)*, Ossinodus* (Warren and Turner 2004) and *Pederpes* (Clack and Finney 2005) (FF, Fig. 5D), and in the crown tetrapods *Archeria* (Romer 1957) and *Eryops* (Pawley and Warren 2006). If the fibular fossa does represent the origin of *flexor digitorum longus,* it would imply that the crural portion of the superficial ventral musculature was separate from the thigh portion in the LCA of tetrapods. In further support of this conclusion, a ventral fibular ridge (VRFib, Figs. 4F and 5F) is also present in most early tetrapods (Table S3), representing the origin of the *flexor* *accessorius lateralis,* which gave rise to the fibular head of *flexor digitorum longus* in amniotes. Also in stem tetrapods is the first appearance of the ventral crest of the tibia (VCT, Fig. 4F), interpreted as the insertion of *gracilis* and/or *ischioflexorius* in the stem tetrapod *Greererpeton* (Godfrey 1989) and the crown tetrapods *Eryops* (Romer 1922) and *Proterogyrinus* (Holmes 1984), implying that in the LCA of tetrapods the proximal portion of the superficial ventral musculature was fully separate from the middle portion. Subsequently, each muscle mass followed its own evolutionary pattern of differentiation into the individual muscles found in modern crown tetrapods.

Deep ventral musculature

The deep ventral musculature of the pelvic appendage in *Latimeria* and *Neoceratodus,* consisting of the *abductor profundus* and a series of pronators, is an almost perfect mirror image of the deep dorsal musculature (Fig. 1). Presumably, the LCA of crown-group sarcopterygians had a similar configuration (Diogo et al. 2016); however, the limited fossil evidence yields an equivocal character state for this node (Table S4). In the tetrapodomorph fish *Eusthenopteron,* a concavity "probably homologous with the tetrapod intertrochanteric fossa" (ITF, Figs. 3D, 4D, 5D) appeared on the proximal ventral femur (Andrews and Westoll 1970, p. 226). This area was interpreted as the insertion of *puboischiofemoralis externus* in stem tetrapods such as *Ichthyostega* (Ahlberg 2011), *Crassigyrinus* (Panchen and Smithson 1990), and *Greererpeton* (Godfrey 1989), as well as most of the crown tetrapods we studied including *Iguana* (Russell and Bauer 2008) and *Sphenodon* (Dilkes 1999). Therefore, this muscle or its homologue *abductor profundus* was probably present in the LCA of *Eusthenopteron* and more crownward tetrapodomorphs. However, it is unclear whether or not an intertrochanteric fossa was present in *Panderichthys,* and no femur is preserved in *Tiktaalik*; further fossil evidence will help to determine the evolutionary timing and pattern of this feature. In all stem tetrapod femora we studied, an adductor crest (AdC, Figs. 4D and 5D) – which marks the insertion of *adductor femoris* (Smithson 1985; Holmes 2003) – was present, suggesting that in the LCA of tetrapods the *abductor profundus* was replaced by *adductor femoris* and *puboischiofemoralis externus.* Finally, in the stem tetrapod *Crassigyrinus* (Panchen and Smithson 1990) and the crown tetrapods *Archeria* (Romer 1957) and *Captorhinus* (Holmes 2003)*,* ridges on the opposing faces of the tibia and/or fibula are interpreted as the attachments of "interosseous ligaments and musculature" on the tibia (Romer 1957, p. 135) and the *popliteus* (a derivative of *interosseous cruris*; Hutchinson et al. 2002; Diogo et al. in press) on the fibula (Holmes 2003, p. 519). Because the *interosseous cruris* is hypothesized to be homologous with the *supinator 2* of lobe-finned fish, the presence of these ridges supports the presence of this muscle in the LCA of crown tetrapods.

DISCUSSION

Comparisons with previous studies

Several previous studies have attempted to reconstruct appendicular muscle anatomy in early tetrapods and their relatives, although most have focused on the pectoral appendage (Romer 1924; Miner 1925; Andrews and Westoll 1970; Holmes 1977; e.g., Ahlberg 1989; Bishop 2014; Molnar et al. 2017a). Exceptions include reconstructions of the hindlimb anatomy in the Permian amniotes *Diadectes* (Romer 1922) and *Labidosaurus* (Sumida 1989), but to our knowledge the present study is the first detailed attempt to reconstruct the evolution of pelvic musculature in tetrapodomorph fish or stem tetrapods. The muscle homology hypotheses upon which our reconstructions are based come from Diogo et al. (2016), which compared extant sarcopterygian fish (*Neoceratodus* and *Latimeria*) and tetrapods *(Ambystoma).* Their proposed homology hypotheses were based upon: 1) embryonic primordia and sequence of development (from *Neoceratodus* and *Ambystoma*, Boisvert et al. 2013; Diogo and Tanaka 2014); 2) comparative anatomy including architecture, innervation, topology, and attachments; and 3) distribution of muscles within the phylogeny of each group (see Diogo et al. 2016 for detailed methods). Boisvert et al. (2013) has also previously proposed muscle homologies between the same three taxa. On most points the two studies agree, but in several cases Boisvert et al. (2013) proposed homologies between a dorsal muscle and a ventral muscle, whereas Diogo et al. (2016) homologized dorsal muscles only with other dorsal muscles. For example, the former study suggested that the lateral part of the ventral muscle *pterygialis caudalis* of *Neoceratodus* ("superficial ventrolateral adductor" sensu Young et al. 1989) is homologous with the dorsal muscle *gracilis* ("puboischiotibialis") of *Ambystoma,* and also that the dorsal pronators 1-3 in *Latimeria* are homologous with the ventral muscle "deep ventral adductor depressor" (supinator 1) in *Neoceratodus*. We consider such homologies between dorsal and ventral muscles to be unparsimonious and implausible.

Variation and outliers

Many osteological correlates of muscle attachment are shared among closely related taxa. However, some taxa have relatively featureless skeletons, while others have an unusual number of markings and prominences. Some of this interspecific variation seems to be related to mode of life. For example, the femur of the aquatic stem tetrapod *Crassigyrinus* lacks a well-defined intertrochanteric ("adductor") fossa and has no adductor crest, but its internal trochanter is unusually large, and only a shallow groove separates it from the fourth trochanter (Panchen and

Smithson 1990). The femur of the stem tetrapod *Pederpes* is similar in that it also has a poorly defined intertrochanteric fossa and adductor crest; this morphology is thought to indicate a juvenile stage and/or aquatic mode of life (Clack and Finney 2005). *Pederpes* is also unusual among stem tetrapods in lacking an ossified pubis, clear separation between the femoral head and shaft, and cnemial and ventral crests of the tibia. On the other end of the spectrum, the skeleton of the amphibian *Eryops* displays many specialized features in addition to those common to most of the other tetrapods we studied. Unique markings include an intercondylar crest, posterior intertrochanteric ridge, and anterior popliteal ridge on the femur, as well as several ridges on the tibia and fibula (Pawley and Warren 2006). Because this taxon is much larger and more heavily built than most tetrapods we studied, these bony characteristics probably reflect unusually well-developed musculature (i.e., scaling influences and sheer size causing features to be more visible) rather than differences in muscle anatomy. Other osteological features seem to be species-specific without any obvious homology. For instance, the femur of *Panderichthys* is marked with parallel longitudinal ridges, presumably for muscle attachment, but such an attachment is not found in either tetrapods or in *Eusthenopteron* (Boisvert 2005), the only other tetrapodomorph fish with a well-preserved femur.

Pelvic vs. pectoral appendicular musculature

Comparison of the results of this study with similar data from the pectoral appendage (Molnar et al. 2017a) supports the hypothesis that the pectoral appendage of early tetrapods had slightly more differentiated musculature than the pelvic appendage at each node in the phylogeny – as suggested by Boisvert (2005) and Pierce et al. (2013b) – or at least a greater number of distinct osteological correlates. For example, in the LCA of all tetrapods the forelimb is reconstructed with 19 individual muscles, while the hindlimb is reconstructed with only 17

(Table 3). The reason for this disparity is that fewer osteological correlates of muscle attachment were identified on the femur, tibia, and fibula than on the humerus, radius and ulna. This difference is greatest in early tetrapods (although still very small, and also very sensitive to our ability to identify osteological correlates); in the LCA of crown tetrapods, the number of muscles is 20 for the forelimb and 19 for the hindlimb, and in the LCA of tetrapodomorphs both appendages are reconstructed with 13 muscles. In the latter case, the reconstructions are influenced by the inclusion of the modern lungfish *Neoceratodus,* which has much simpler musculature in the pectoral fin than the pelvic fin, probably due to secondary reduction within the evolutionary history of dipnoans (Diogo et al. 2016). More striking than the difference in number of muscles is their location: the hindlimb of the LCA of tetrapods as reconstructed here has many more hip/thigh than shank muscles (eight versus three), whereas the number of muscles of the forelimb segments are more balanced (seven versus six) (Molnar et al. 2017a) (Table 3). This evidence supports the hypothesis that the transformation of the pelvic appendage lagged behind that of the pectoral appendage in early tetrapods and their closest relatives (Boisvert 2005; Clack 2009; Pierce et al. 2013b), particularly in the distal region, whereas in more crownward taxa changes in the pelvic limb dominated (Coates et al. 2002; Swartz 2012).

In addition to number of muscles, the pelvic and pectoral appendages of stem tetrapods appear to have differed in muscle configuration. Eleven hindlimb muscles were reconstructed in the LCA of all tetrapods, but only seven (64%) of them show clear "topological correspondence" with muscles of the forelimb, and of those only two are zeugopodial muscles (Table 3). "Topological correspondence" refers, here, to muscles like the *triceps* in the arm and the *quadriceps femoris* in the thigh that have similar origins, insertions, relative position, architecture, and embryonic origins (Diogo and Molnar 2014). In terms of total percentages, the results of our study seem to contradict the prediction of, e.g., Diogo and Molnar (2014), that there was a similarity bottleneck in stem tetrapods driven by the appearance of similar structures (i.e. leg-forearm and foot-hand) in the distal limb (but see caveats in the next paragraph). As described in that study, a similarity bottleneck is a node in the phylogeny at which the muscles of the pectoral appendage and the muscles of the pelvic appendage are thought to have been more similar than they were at more basal or more crownward nodes. If the total number rather than percentage of similar muscles is used as a metric for similarity, even within our sample - excluding autopodial muscles - the pectoral and pelvic appendages as reconstructed in the LCA of tetrapods do appear overall more similar to each other than those of the LCA of tetrapodomorphs or sarcopterygians (seven similar muscles compared with four and three similar muscles, respectively), but those of the LCA of crown tetrapods are even more similar (nine similar muscles).

These results call into question the idea of a similarity bottleneck at the origin of tetrapods, but they do not exclude it as a possibility. For one thing, the present analysis does not include autopodial muscles, because few if any osteological correlates of these muscles are preserved in the fossil record, while the similarity bottleneck proposed by Diogo & Molnar (2014) was mainly due to similarity between the forelimb and hindlimb zeugopodial and autopodial muscles. Therefore, if autopodial muscles had been included in our study, they would probably have increased the total number of similar muscles and likely also the percentage of similar muscles in tetrapods (although this is also true of crown tetrapods). Future scrutiny of unusually well preserved fossil autopodia might be able to test this possibility more conclusively. Also, the similarity bottleneck described by Diogo and Molnar (2014) was based on comparison between extant fish and extant tetrapods, so the bottleneck and associated genetic and developmental changes to which they referred to explain this bottleneck might have occurred at any point between the origin of sarcopterygians and the origin of crown tetrapods (their Figure 2).

Gregory (1928) and, more recently, Diogo et al. (2016) predicted the existence of a second, earlier bottleneck at the origin of crown sarcopterygians, resulting in more similar muscular configurations of the pectoral and pelvic fins in these fishes than are present in most non-sarcopterygian fishes (Figure 4 of Diogo et al. 2016). Comparison of the results from the present study with our previous study of the pectoral appendage (Molnar et al. 2017a) supports this hypothesis: the LCA of crown sarcopterygians as reconstructed here has a greater percentage of similar muscles (75%) than any other node in the phylogeny, or any of the extant taxa analyzed here except for *Ambystoma* (81%) (Table 3). However, the LCA of chondrichthyans has 60% (three) similar muscles (Diogo and Ziermann 2015), and that of the early diverging osteichthyan *Polypterus* has 77% (five) similar muscles (Diogo et al. 2016; Molnar et al. 2017b). Therefore, strictly in terms of percentage, the fins of the LCA of crown sarcopterygians do not represent a bottleneck in the sense of being more similar to each other than those of most other fish.

In the light of these numbers, the utility of comparing percentages seems questionable in cases where the total number of muscles is very small. In fact, one of the main reasons that Diogo et al. (2013) used the total number of muscles when discussing the hindlimb-forelimb similarity bottlenecks was that, if one were to strictly apply percentages, then pelvic and pectoral fins with only two muscles each, an adductor and an abductor mass, would be 100% similar. However, the similarity between two fins with only abductor and adductor muscle masses is not as striking as that seen between the distal regions of the forelimb and hindlimb in tetrapods such as salamanders and humans, where up to 19 muscles of each limb are remarkably similar to the ones of the other limb (Diogo et al. 2013; Diogo and Molnar 2014). Therefore, it is probably more informative to take into account *both* the percentage and the total number of muscles, as we do here.

Implications for appendicular function

Most modern, quadrupedal terrestrial tetrapods produce locomotor thrust with their hindlimbs, while the forelimbs contribute to body support and braking (e.g., crocodylians: Willey et al. 2004; salamanders: Kawano and Blob 2013). On the contrary, the limbs of early tetrapods may have exhibited considerable functional diversity. For example, in *Ichthyostega* the forelimb is thought to have generated forward motion through a crutching motion against the substrate, while the hindlimb was mainly used in swimming (Ahlberg et al. 2005; Pierce et al. 2012, 2013a). A "front-wheel drive" gait, powered mainly by body flexion, was postulated in *Panderichthys* because of the aforementioned size differences between its pectoral and pelvic appendages (Vorobyeva and Kuznetsov 1992; Boisvert 2005), and also in *Eusthenopteron* (Andrews and Westoll 1970). A similar gait was suggested as being characteristic of the earliest terrestrial tetrapods (Gregory 1928). One author suggested based on trackways (and on a study of sub-aqueously "walking" sharks) that the gait of early tetrapods was a trot or a lateral-sequence walk (Pridmore 1995). However, Clack (1997) reviewed supposed Devonian tetrapod trackways and concluded that currently known Devonian stem tetrapods were unlikely to have produced them, unless they were underwater. In particular, it was noted that the Genoa River trackways, which are among the most convincingly tetrapod-like, show a manus and pes directed at right angles to the body (i.e., with no evidence of supination), and thus more characteristic of a paddle-like stroke than the powerstroke of a walking tetrapod. Incongruously, recently discovered sets of trackways from Poland that pre-date any tetrapod body fossils show a manus and pes oriented anterolaterally (Niedźwiedzki et al. 2010), and, based on a recent sedimentological analysis, it was suggested that their makers may have been capable of terrestrial locomotion (Qvarnström et al. 2018).

The relatively small number of muscles reconstructed in the hindlimb's zeugopod relative to the forelimb's zeugopod in the LCA of tetrapods (three versus six) supports the hypothesis that the hindlimbs of the earliest tetrapods functioned mainly as paddles (e.g., Coates and Clack 1995; Pierce et al. 2012, 2013b; Clack 2012). Conspicuously absent as separate muscles in the reconstruction of hindlimb musculature in the Devonian tetrapod *Acanthostega* (Fig. 7B, D) are the crural muscles *extensor cruris tibialis, extensor tarsi tibialis* (homologous with the amniote *tibialis anterior*; Table 1), and *extensor cruri et tarsi fibularis* (homologous with the amniote muscles *fibularis longus* and *brevis*). In lizards and salamanders, these muscles are thought to produce not only flexion and extension of the ankle and crus, but also ankle abduction (*tibialis anterior* in lizards; Reilly 1995), supination of the foot (*extensor tarsi tibialis* in salamanders; Francis 1934), and abduction of the fibula/crus *(extensor cruri et tarsi fibularis* in salamanders; Francis 1934). These muscles therefore assist in controlling the distal limb in complex three-dimensional motions, including applying multi-directional forces against the substrate during terrestrial locomotion. The acquisition of crural muscles in stem tetrapods crownward of *Acanthostega* and *Ichthyostega* (nodes 4 and 5 of Fig. 7) would presumably have allowed them to perform functions such as supinating the foot before touch-down so that the plantar surface faces the substrate, as do extant amphibians and reptiles (Schaeffer 1941; Brinkman 1981; Ashley-Ross 1995). Notably, tetrapod-like gaits can also be produced by animals with very different musculature: for example, the lungfish *Protopterus* can produce a tetrapod-like walking gait underwater despite having only two pelvic appendicular muscles (King et al. 2011; Aiello et al. 2014). However, terrestrial locomotion also requires the ability to overcome much greater effects of gravity and friction, implying that the acquisition of complex musculature spanning the knee and ankle was an important step in the conquest of land.

CONCLUSIONS

Our study has found that the evolution of tetrapod hindlimb muscles lagged behind that of the forelimb, in keeping with osteological evidence. In particular, osteological correlates of muscle attachment appear on the forearm several nodes below where they appear on the shank. This result supports the hypothesis that the pelvic appendage remained more fin-like in the earliest tetrapods even as the pectoral appendage became limb-like. Similarity between the pectoral and pelvic appendages in terms of the number of topologically similar muscles increased steadily from the LCA of crown sarcopterygians to the LCA of crown tetrapods, and this similarity is greatest in *Ambystoma* among the taxa included in this study. However, the total number of appendicular muscles also increased, so that the percentage of topologically corresponding muscles actually decreased. Neither the trend in percentage nor the trend in total number of similar muscles directly supports the hypothesis of a "similarity bottleneck" at the origin of tetrapods as previously proposed (e.g., Diogo and Molnar 2014), although this result might have been different had autopodial muscles been included in our study. Future studies of well-preserved fossil autopodia are needed to better test for hindlimb-forelimb similarity bottleneck(s) in tetrapod evolution.

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TABLE CAPTIONS

Table 1. Hypotheses of homology between pelvic appendicular muscles of extant taxa[1],[2].

Table 2. Taxa and specimens included in this study.

Table 3. Topological correspondences[3] between pelvic and pectoral appendicular muscles.

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[1] from Diogo et al.(2016).

[2] Muscles in grey are located in parts of the appendage not included in the current analysis

[3] "Topological correspondences" refers to muscles that have similar origins, insertions, relative position, architecture, and embryonic origins (Diogo and Molnar 2014).

FIGURE CAPTIONS

Figure 1.

Hypotheses of hindlimb muscle homology from Diogo et al. (2016). (A, B) *Latimeria*, (C, D) *Neoceratodus*, and (E, F) *Ambystoma* in dorsal (A, C, E) and ventral (B, D, F) views. Colors indicate homologous muscles. Abbreviations: *abductor digiti minimi* (AbD5), *abductor dorsolateralis* (AbDL), *abductor et extensor digit 1* (AbED1), *abductor profundus* (AbP), *abductor superficialis* (AbS), *adductor profundus* (AdP), *adductor superficialis* (AdS), *caudofemoralis* (CdF), *contrahentium caput longum* (CCL), *elevator lateralis* (EL), *extensor cruri et tarsi fibularis* (ECTF), *extensor cruris tibialis* (ECT), *extensor digitorum longus* (EDL), *extensor iliotibialis* (ExIlT), *extensor tarsi tibialis* (ETT), *femorofibularis* (FmFb), *flexor accessorius lateralis* (FAL), *flexor accessorius medialis* (FAM), *flexor digitorum longus* (FDL), *gracilis* (G), *interosseous cruris* (IOC), *ischioflexorius* (IsF), *pronator* (Pr), *pronator profundus* (PP), *pterygialis cranialis* (PtCr), *pterygialis caudalis* (PtCd), *puboischiofemoralis externus* (PIFE), *puboischiofemoralis internus* (PIFI), *pubotibialis* (PTb), *supinator* (S).

Figure 2.

Muscle attachment areas on the right pelvic appendages of *Neoceratodus* (A-F; modified from Diogo et al. (2016)), *Latimeria* (G-L; modified from Diogo et al. (2016)), *Salamandra* (M-R; modified from Francis (1934)), and *Iguana* (S-X; modified from Dilkes (1999)). Abbreviations: *adductor femoris* (AdFm), *ambiens* (Amb), *femorotibialis* (FmTb), *fibularis* (Fb), *flexor tibialis internus* (FTI), *iliofemoralis* (IlFm), *ischiotrochantericus* (IsTr), *tenuissimus* (T), *tibialis anterior*

(TA), Colours and other abbreviations as in Figure 3. Silhouettes show configuration of pelvic girdle and proximal fin bones in *Neoceratodus* and *Salamandra.*

Figure 3.

Osteological correlates of muscle attachment in the pelvic appendage of *Eusthenopteron.* Pelvis in A) lateral and D) medial views, femur in B) dorsal and E) ventral views, and tibia and fibula in C) dorsal and F) ventral views. Abbreviations: acetabulum (A), dorsal ridge of femur (DRFem), intertrochanteric fossa (ITF), mesial process (MP), posteroventral process (PVP), ventral ridge of femur (VRFem).

Figure 4.

Osteological correlates of muscle attachment in the pelvic appendage of *Acanthostega.* Pelvis in A) lateral and B) medial views, femur in C) dorsal and D) ventral views, and tibia and fibula in E) dorsal and F) ventral views. Abbreviations: acetabulum (A), adductor crest (AdC), cnemial crest (CC), fourth trochanter (T4), intercondylar fossa (ICF), internal trochanter (InT), intertrochanteric fossa (ITF), medial ridge of pelvis (MRPel), popliteal fossa (Pop), posterior iliac process (PIP), transverse line of ilium (TLI), ventral ridge of fibula (VRFib).

Figure 5.

Osteological correlates of muscle attachment in the pelvic appendage of *Pederpes.* Pelvis in A) lateral and B) medial views, femur in C) dorsal and D) ventral views, and tibia and fibula in E) dorsal and F) ventral views. Abbreviations: adductor crest (AdC), cnemial crest (CC), fourth trochanter (T4), intercondylar fossa (ICF), internal trochanter (InT), intertrochanteric fossa (ITF), medial ridge of pelvis (MRPel), popliteal fossa (Pop), posterior iliac process (PIP), ventral crest of tibia (VCT), ventral ridge of fibula (VRFib).

Figure 6.

Hypothetical sequence of muscle differentiation from superficial and deep dorsal and ventral muscle masses based on the results of mapping osteological correlates onto on the phylogeny of Ruta et al. (2003) and Ruta (2011). See text for specific osteological correlates. Colors correspond to Fig. 1. Dashed lines indicate partial separation of muscles by tendinous intersections. Muscles in grey text and greyed-out portions of muscles indicated by horizontal bars are inferred to be present based on homology but not associated with osteological correlates. Numbers 1–6 along the bottom of the figure indicate key nodes along the phylogeny discussed in the text. "+" indicates muscles that are part of larger muscle masses. Muscles listed on the right are hypothesized to be plesiomorphic for crown-group tetrapods (Diogo et al. in press and references therein). Abbreviations: QF (*quadratus femoris*).

Figure 7.

Reconstructions of muscle anatomy in the right fore- and hindlimbs of the tetrapodomorph fish *Eusthenopteron foordi* (Andrews and Westoll 1970, p. 226) (A, C) and the stem tetrapod *Acanthostega gunnari* (Coates 1996) (B, D). Forelimb reconstructions based on Molnar et al. (2017a). Medial (A) and lateral (B) views shown. * indicates area of origin uncertain; **area of insertion uncertain. Colors correspond to Figure 1. Muscles in grey text are inferred to be present based on homology but not associated with individual osteological correlates.

Tables

Table 1. Hypotheses of homology between pelvic appendicular muscles of extant taxa[4],[5].

Muscle groups	***Latimeria***	***Neoceratodus***[6]	***Ambystoma***	***Timon***
Abaxial, and partially primaxial?[7]	Levator lateralis	Abductor dorsolateralis ('superficial ventrolateral abductor')	Caudofemoralis	Caudofemoralis longus
				Caudofemoralis brevis
Adductor superficialis (superficial dorsomesial musculature)	Adductor superficialis ('levator superficialis')	Adductor superficialis ('mesial adductor' + superficial dorsal segmented layer that corresponds to 'dorsal lepidrotrichial flexors + radial flexors')	Extensor iliotibialis ('iliotibialis')	Iliotibialis
				Femorotibialis
				Sartorius ('ambiens')
			Extensor cruris tibialis	Tibialis anterior
			Extensor tarsi tibialis	
			Extensor digitorum longus	Extensor digitorum longus
	Pterygialis caudalis (postaxial muscle, or 'pelvic adductor')	Pterygialis caudalis (postaxial muscle, or 'superficial ventrolateral + ventromesial adductor')	Extensor cruris et tarsi fibularis	Fibularis longus
				Fibularis brevis
			Tenuissimus ('iliofibularis')	Tenuissimus ('iliofibularis')
Adductor profundus (deep dorsomesial musculature)	Adductor profundus ('levator profundus)	Adductor profundus ('dorsomesial adductor-levator')	Puboischiofemoralis internus	Puboischiofemoralis internus
	Pronator 1	Pronator 1	Iliofemoralis	Iliofemoralis
	Pronator 2	Pronators 2-9 (dorsal 'radial-axial' muscles)	Abductor et extensor digit 1	Abductor et extensor digit 1
	Pronator 3		Extensores digitorum breves 2-5	Extensores digitorum breves 2-5
	Pronator 4			
Abductor superficialis (superficial ventrolateral musculature)	Abductor superficialis ('abaisseur' superficialis)	Abductor superficialis ('superficial ventromesial abductor' + superficial ventral segmented layer that corresponds to 'ventral lepidrotrichial flexors + radial flexors')	Gracilis ('puboischiotibialis')	Gracilis ('puboischiotibialis')
			Flexor digitorum communis	Gastrocnemius externus
				Gastrocnemius internus
				Flexor digitorum longus, proximal head
			Pubotibialis (?)	Pubotibialis (?)
			Femorofibularis (?)	
	Pterygialis cranialis (preaxial muscle, or 'pelvic abductor')	Pterygialis cranialis (preaxial muscle, or part of 'superficial	Ischioflexorius[8]	Flexor tibialis internus
				Flexor tibialis externus

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[4] from Diogo et al.(2016).

[5] Muscles in grey are located in parts of the appendage not included in the current analysis

[6] Muscle names from Young et al. (1989) given in quotation marks

[7] Included here because of origin from axial skeleton/muscles, but direct homology with lateral levator of *Latimeria* and/or dorsolateral abductor of *Neoceratodus* is not assumed, as the muscle of *Latimeria* is seemingly part of dorsal musculature, while caudofemoralis is part of ventral musculature.

[8] Likely includes flexor cruris et tarsi tibialis, and perhaps femorofibularis + pubotibialis

		ventromesial abductor')		
Abductor profundus (deep ventrolateral musculature)	Abductor profundus ('abaisseur' profundus)	Abductor profundus ('deep ventral abductor-depressor')	Adductor femoris (pubifemoralis)	Adductor femoris (pubifemoralis)
			Puboischiofemoralis externus	Puboischiofemoralis externus
	Supinator 1	Supinator 1 ('deep ventral adductor-depressor')	Ischiotrochantericus ('ischiofemoralis')	Ischiotrochantericus ('ischiofemoralis')
	Supinator 2	Supinators 2-9 (ventral 'radial-axial' muscles)	Flexor accessorius medialis	Flexor digitorum longus, distal head
			Tibialis posterior ('pronator profundus')	Tibialis posterior ('pronator profundus')
			Interosseous cruris	Popliteus
				Interosseous cruris
	Supinator 3		Flexor accessorius lateralis	Flexor digitorum longus
	Supinator 4		Contrahentium caput longum	

Table 2. Taxa and specimens included in this study.

Genus and species	Clade	Specimen(s) examined[9]	Preserved pelvic elements[10]	References
Extant taxa				
Latimeria chalumnae	Coelacantha	EKUT CCC162.11, CCC161	N/A	Diogo et al.(2016); Millot & Anthony (1958)
Neoceratodus forsteri	Dipnoi	MQU JVM-I-1051NC, JVM-I-1052NC	N/A	Braus (1900); Young *et al.* (1989); Diogo et al.(2016)
Protopterus annectens	Dipnoi		N/A	King & Hale (2014)
Salamandra salamandra	Lissamphibia	RVC JRH-SAL1 through SAL5	N/A	Francis (1934)
Ambystoma mexicanum	Lissamphibia	HU AM1, HU AM2	N/A	Diogo & Tanaka (2014)
Sphenodon punctatus	Rhynchocephalia	BMNH 1969.2204, BMNH 1935.12.6.1, S1/MEHJ#1, UMZC R2604	N/A	Byerly (1925); Osawa (1898); Russell & Bauer (2008)(Osawa 1898; Byerly 1925; Miner 1925; Russell and Bauer 2008)(Osawa 1898; Byerly 1925; Miner 1925; Russell and Bauer 2008)(Osawa, 1898; Byerly, 1925; Miner, 1925; Russell and Bauer, 2008)(Osawa, 1898; Byerly, 1925; Miner, 1925; Russell & Bauer, 2008)(Byerly, 1925; Miner, 1925; Osawa, 1898; Russell and Bauer, 2008)
Iguana iguana	Squamata	3 specimens; un-numbered	N/A	Russell & Bauer (2008) and references therein
Non-tetrapodomorph sarcopterygians				
Griphognathus	Dipnomorpha		Pelvis	Young *et al.* (1989)
Chirodipterus australis	Dipnomorpha		Pelvis	Young *et al.* (1989)
Glyptolepis sp.	Dipnomorpha		Pelvis; poorly preserved tibia and fibula	Ahlberg (1989)
Tetrapodomorph fish				
Gooloogongia	Rhizodontida		Pelvis	Johanson & Ahlberg

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[9] Institutional abbreviations: Academy of Natural Sciences of Philadelphia, (ANSP), Geological Museum of the University of Copenhagen (MGUH), Museum of Comparative Zoology, Harvard (MCZ), Natural History Museum, London, UK (BMNH), University of Glasgow Hunterian Museum, UK (GLAHM), Universität Tübingen (EKUT), Macquarie University (MQU), The Royal Veterinary College (RVC), Howard University (HU). Specimens listed were examined by Julia Molnar, John Hutchinson, Rui Diogo and/or Stephanie Pierce.

[10] Elements of the pelvic girdle and appendage described in the literature. Only the pelvis, femur, tibia, and fibula were considered.

loomesi				(1998, 2001)
Eusthenopteron foordi	Osteolepidida	NHMUK 6794a, 6794b, 6806; MCZ 8920, 9155, 6509	Pelvis, femur, tibia, fibula	Andrews & Westoll (1970)
Tiktaalik roseae	Elpistostegalia		Pelvis	Shubin *et al.* (2014); Ahlberg (2011)
Stem tetrapods				
Acanthostega gunnari	Stegocephalia	MGUH 1227, fn260, T1291	Pelvis, femur, tibia, fibula	Coates (1996); Ahlberg (2011); Pierce et al. (2013a)
Ichthyostega (multiple species)	Stegocephalia		Pelvis, femur, tibia, fibula	Ahlberg (2011); Jarvik (1996); Pierce et al. (2012)
Tulerpeton curtum	Stegocephalia		Ilium, femur, tibia, fibula	Lebedev & Coates (1995)
Crassigyrinus scoticus	Stegocephalia		Ilium, ischium, femur, tibia, fibula	Panchen (1985); Panchen & Smithson (1990)
Ossinodus pueri	Whatcheeriidae		Ilium, femur, tibia	Warren & Turner (2004)
Pederpes finneyae	Whatcheeriidae	GLAHM 100815	Ilium, ischium, femur, tibia, fibula	Clack & Finney (2005)
Whatcheeria deltae	Whatcheeriidae		Poorly preserved pelvis, femur	Lombard & Bolt (1995)
Greerepeton burkemorani	Colosteus	MCZ 9006	Pelvis, femur, tibia, fibula	Godfrey (1989)
Baphetes (multiple species)	Baphetidae		Ilium, femur, tibia, fibula	Milner & Lindsay (1998)
Extinct tetrapods within the crown group				
Archeria (multiple species)	Embolomeri	MCZ 2046, 5651, 2045, 2472, 2066, 2047, 2497	Pelvis, femur, tibia, fibula	Romer (1957)
Eoherpeton watsoni	Embolomeri		Pelvis, partial femur, tibia, fibula	Smithson (1985)
Proterogyrinus scheelei	Embolomeri		Pelvis, femur, tibia, fibula	Holmes (1984)
Eryops (multiple species)	Eryopoidea	MCZ 7789, 7798, 3434, 1858, 1219, 7770, 1937, 1853, 6959, 7797	Pelvis, femur, tibia, fibula	Romer (1922); Pawley & Warren (2006)
Captorhinus aguti	Eureptilia		Pelvis, femur, tibia, fibula	Holmes (Holmes 2003)

Table 3. Topological correspondences[11] between pelvic and pectoral appendicular muscles.

Taxa and clades		**Total number of muscles**				**Number of corresponding muscles**		**Percentage of corresponding muscles**		
Extant		FL stylopod	FL zeugopod	HL stylopod	HL zeugopod	Stylopod	Zeugopod	Stylopod	Zeugopod	Total[12]
	Latimeria	6	9	8	3	6	3	86%	50%	69%
	Neoceratodus	4	2	8	5	4	2	67%	57%	63%
	Ambystoma	10	14	11	12	7	12	67%	92%	81%
	Timon	11	16	12	13	6	8	52%	55%	54%
Extinct[13]	LCA crown tetrapods	7	7	10	6	5	4	59%	62%	60%
	LCA *Tulerpeton* + crown tetrapods	7	7	9	4	5	3	63%	55%	59%
	LCA tetrapods	7	6	8	3	5	2	67%	44%	58%
	LCA *Tiktaalik* + crown tetrapods	5	4	4	2	3	2	67%	67%	67%
	LCA tetrapodomorphs	3	3	3	2	2	2	67%	80%	73%
	LCA crown sarcopterygians	2	2	2	2	2	1	100%	50%	75%

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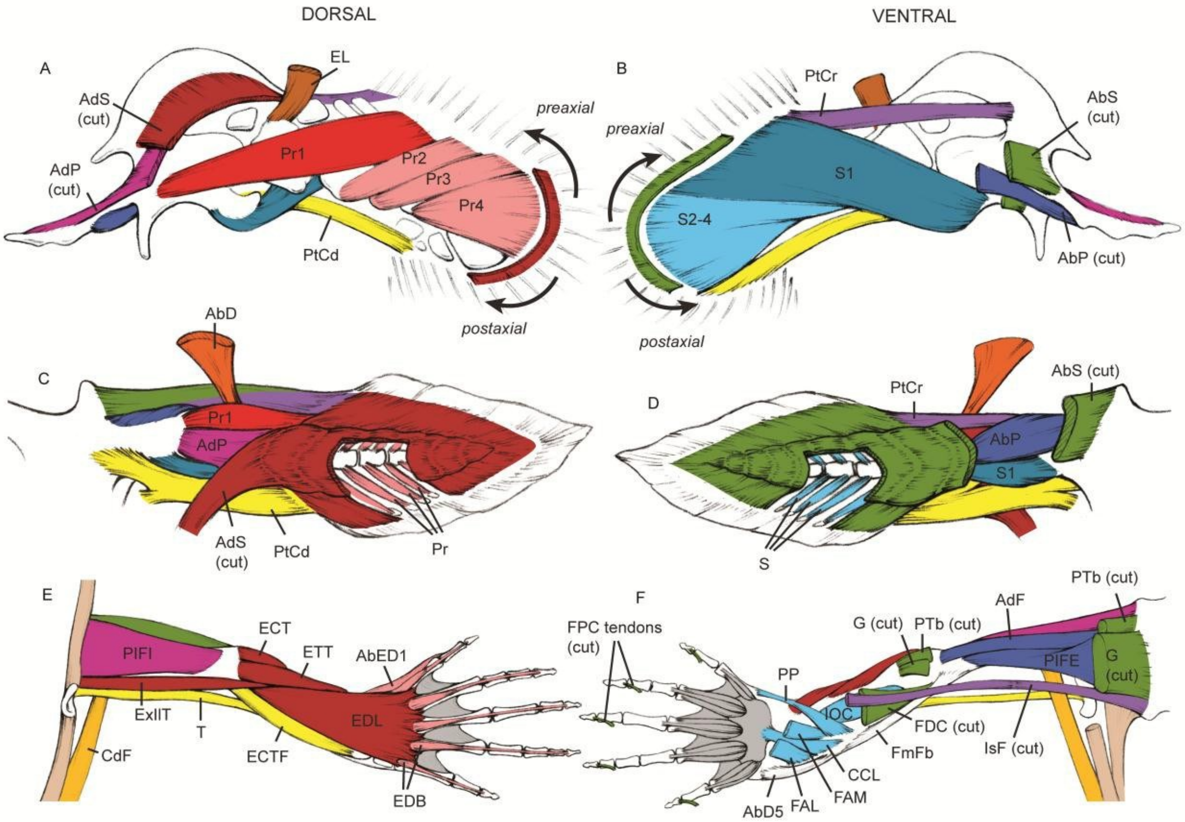
[11] "Topological correspondences" refers to muscles that have similar origins, insertions, relative position, architecture, and embryonic origins (Diogo and Molnar 2014).

[12] Number of corresponding muscles *2 divided by total number of stylopodial and zeugopodial muscles

[13] (Molnar et al. 2017a; this manuscript)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VENTRAL
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PtCr
preaxial
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S2-4
AbS
(cut)
AbP (cut)
postaxial
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AbD
Pr1
AdP
AdS
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PtCd
Pr
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PtCr
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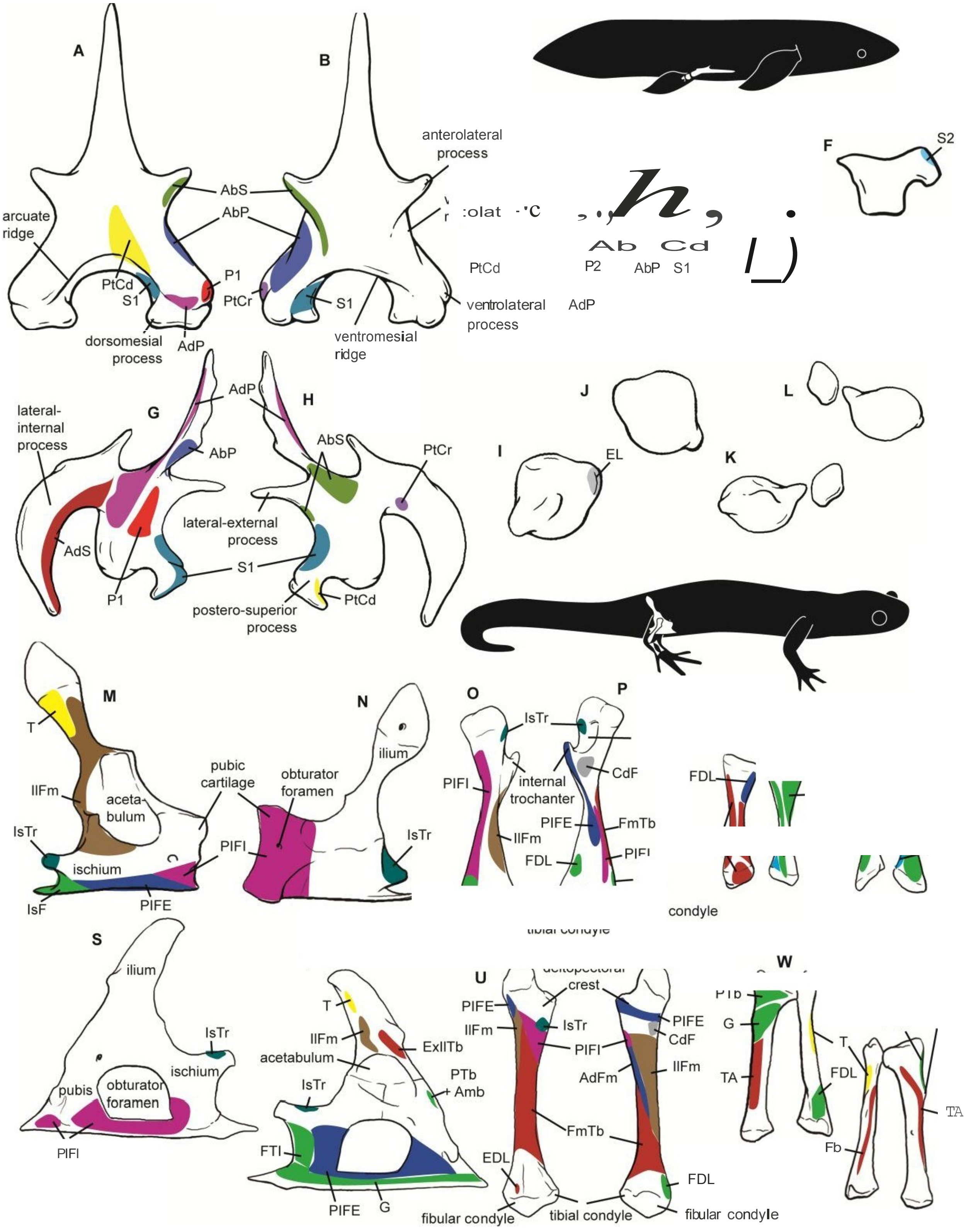
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P2
AbP
S1
AdP
F
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lateral-internal process
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AbP
AbS
PtCr
AdS
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lateral-external process
S1
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obturator foramen
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CdF
IlFm
PIFE
FmTb
FDL
PIFI
FDL
condyle
tibial condyle
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ilium
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ischium
pubis
obturator foramen
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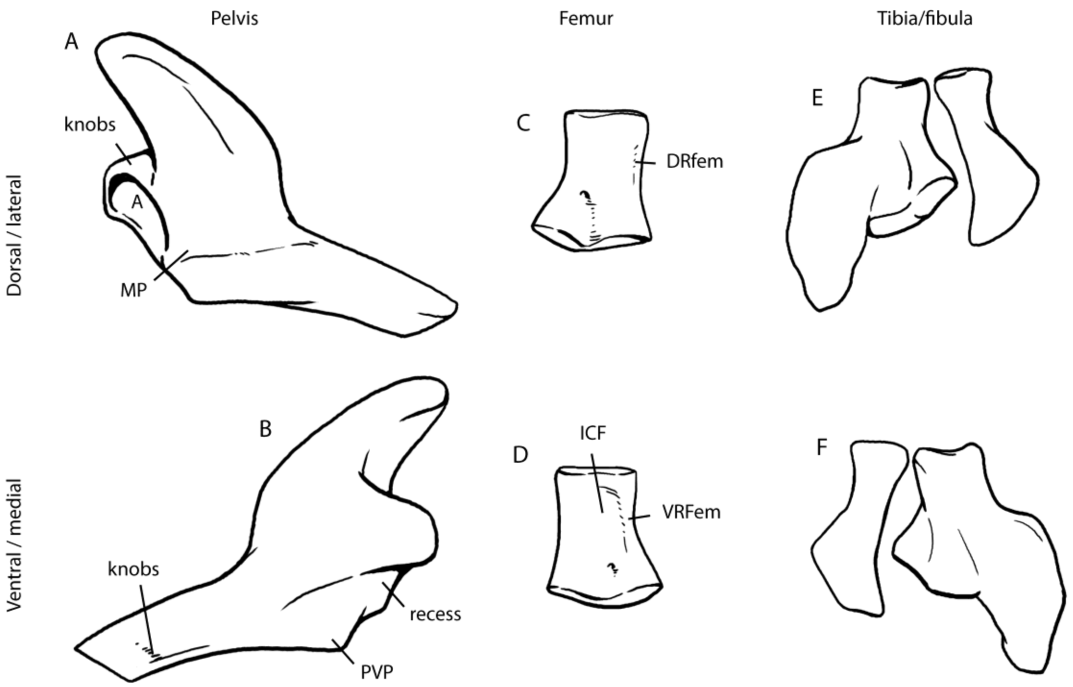
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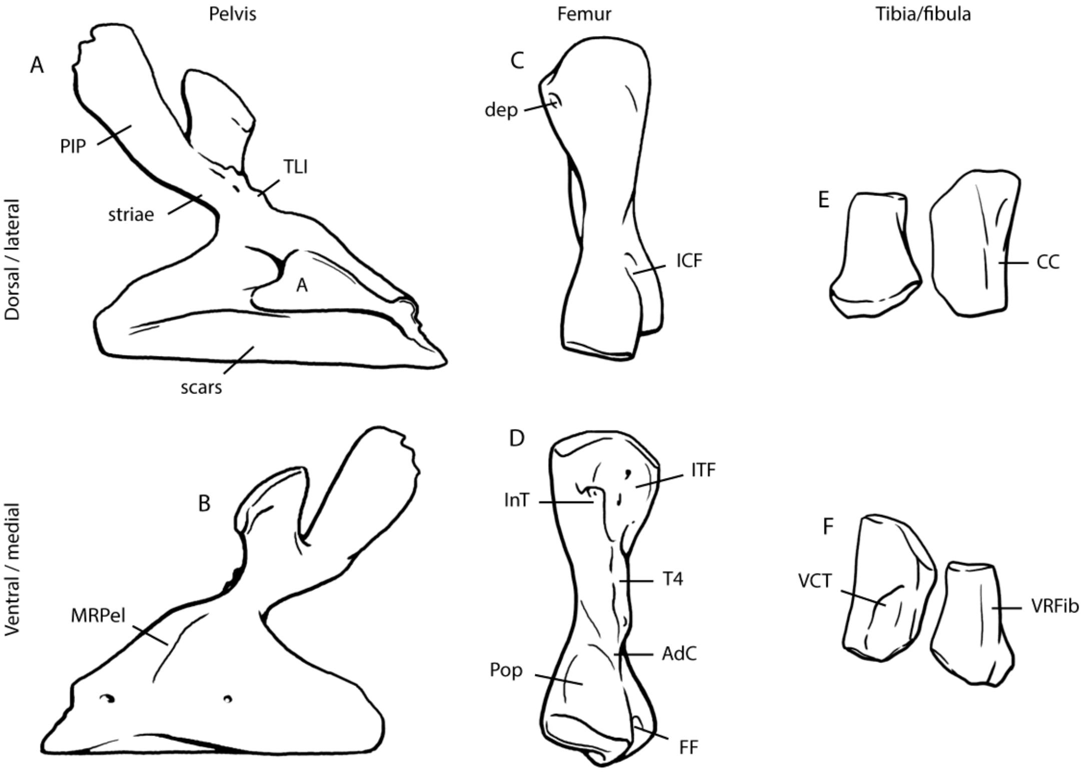
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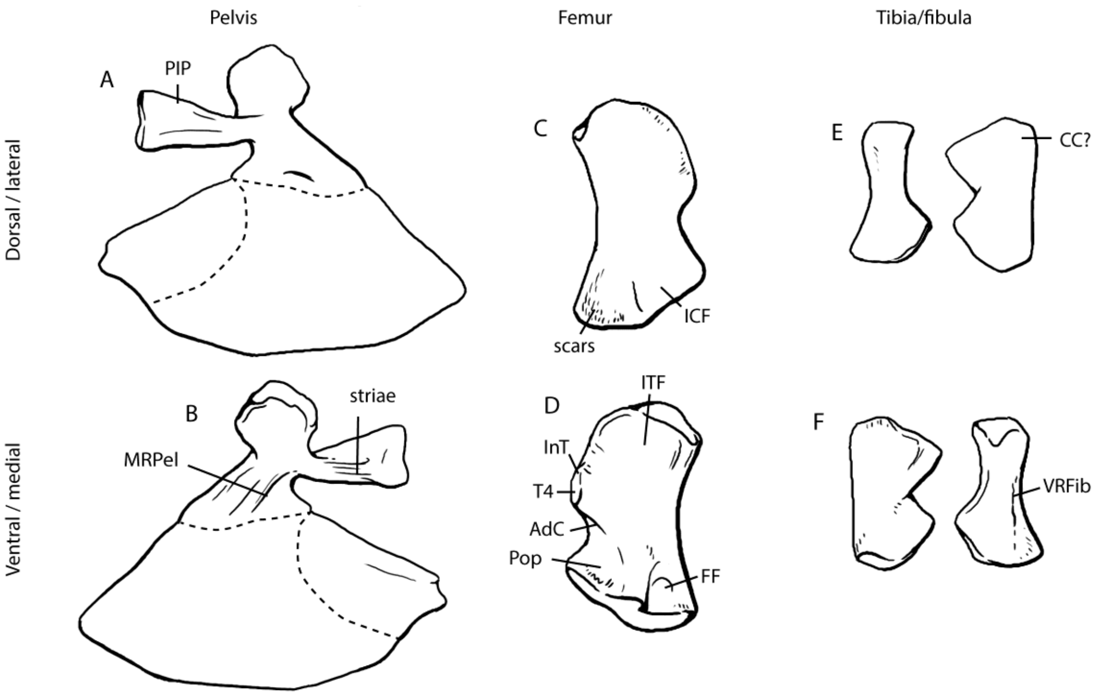
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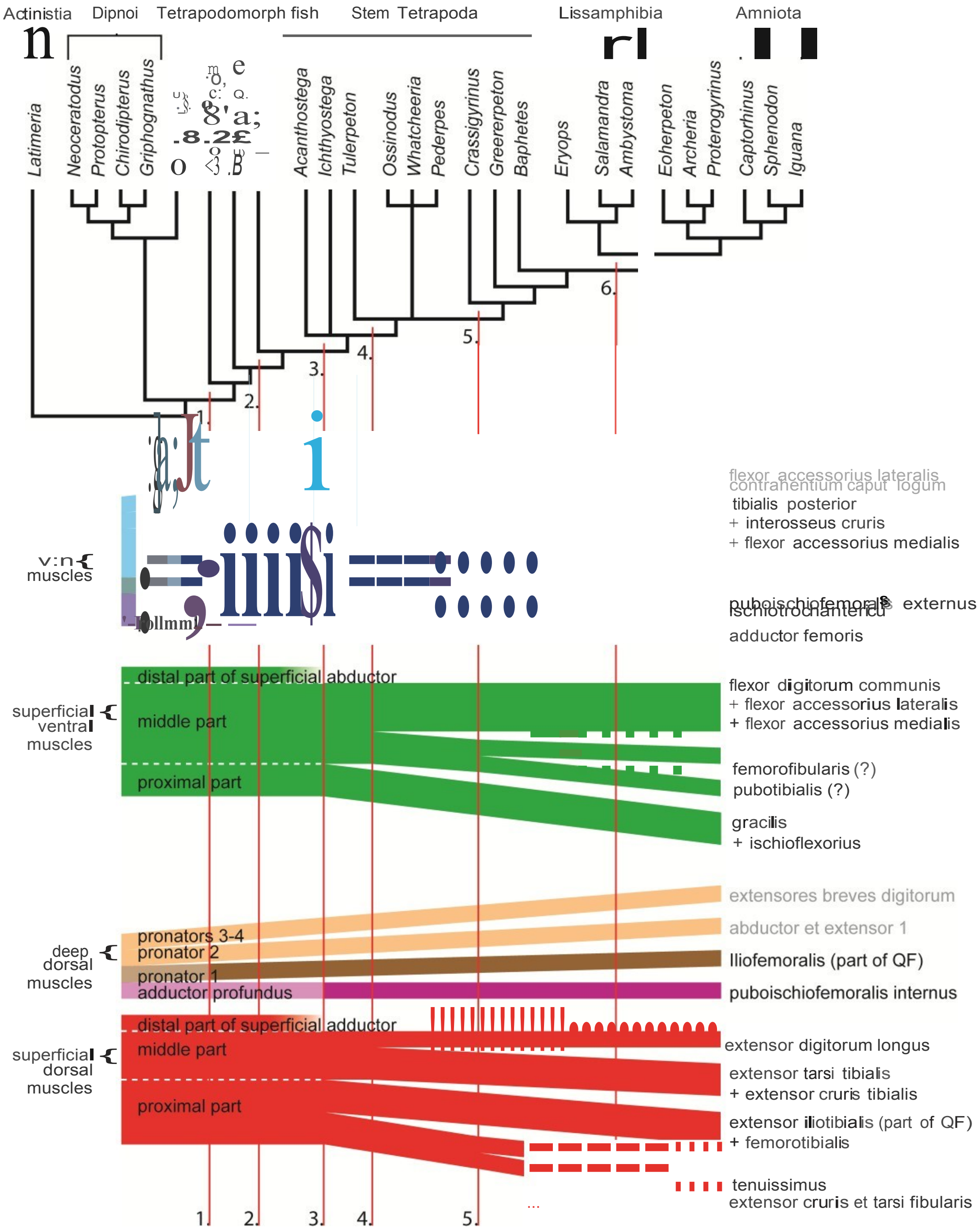
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Tetrapodomorph fish
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Latimeria
Neoceratodus
Protopterus
Chirodipterus
Griphognathus
Acanthostega
Ichthyostega
Tulerpeton
Ossinodus
Whatcheeria
Pederpes
Crassigyrinus
Greererpeton
Baphetes
Eryops
Salamandra
Ambystoma
Eoherpeton
Archeria
Proterogyrinus
Captorhinus
Sphenodon
Iguana
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muscles
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distal part of superficial abductor
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deep
dorsal
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pronator 2
pronator 1
adductor profundus
superficial
dorsal
muscles
distal part of superficial adductor
middle part
proximal part
flexor accessorius lateralis
contrahentium caput logum
tibialis posterior
+ interosseus cruris
+ flexor accessorius medialis
puboischiofemoralis externus
ischiotrochantericu
adductor femoris
flexor digitorum communis
+ flexor accessorius lateralis
+ flexor accessorius medialis
femorofibularis (?)
pubotibialis (?)
gracilis
+ ischioflexorius
extensores breves digitorum
abductor et extensor 1
Iliofemoralis (part of QF)
puboischiofemoralis internus
extensor digitorum longus
extensor tarsi tibialis
+ extensor cruris tibialis
extensor iliotibialis (part of QF)
+ femorotibialis
tenuissimus
extensor cruris et tarsi fibularis
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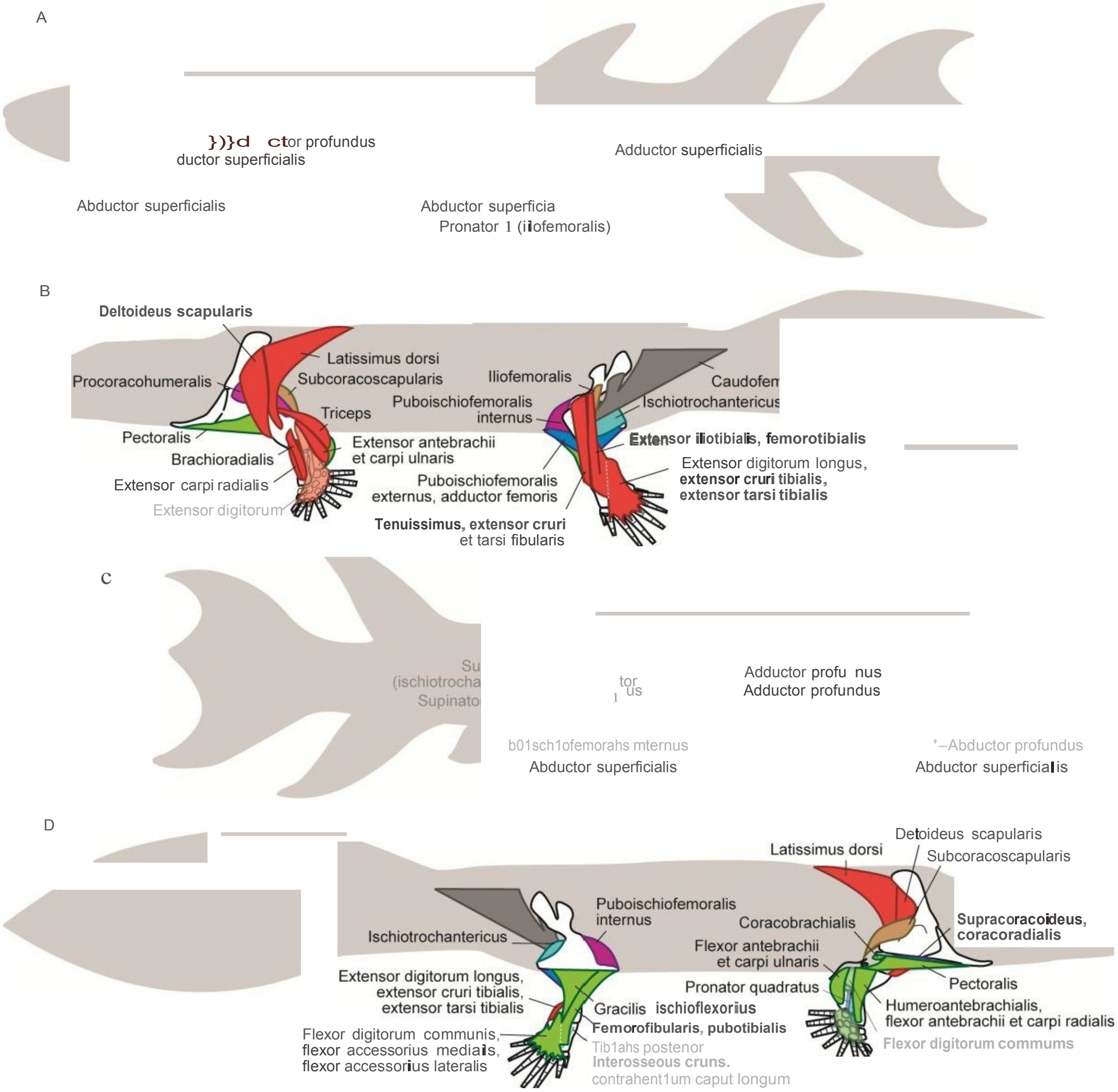A
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Pronator 1 (iliofemoralis)
B
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Latissimus dorsi
Procoracohumeralis
Subcoracoscapularis
Triceps
Pectoralis
Brachioradialis
Extensor carpi radialis
Extensor digitorum
Extensor antebrachii
et carpi ulnaris
Iliofemoralis
Caudofem
Puboischiofemoralis
internus
Ischiotrochantericus
Extensor iliotibialis, femorotibialis
Extensor digitorum longus,
extensor cruri tibialis,
extensor tarsi tibialis
Puboischiofemoralis
externus, adductor femoris
Tenuissimus, extensor cruri
et tarsi fibularis
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Subcoracoscapularis
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Coracobrachialis
Supracoracoideus,
coracoradialis
Ischiotrochantericus
Flexor antebrachii
et carpi ulnaris
Pectoralis
Pronator quadratus
Extensor digitorum longus,
extensor cruri tibialis,
extensor tarsi tibialis
Gracilis ischioflexorius
Humeroantebrachialis,
flexor antebrachii et carpi radialis
Femorofibularis, pubotibialis
Flexor digitorum commums
Flexor digitorum communis,
flexor accessorius medialis,
flexor accessorius lateralis
Tib1ahs postenor
Interosseous cruns.
contrahent1um caput longum