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Comparative Anatomy, Evolution, and Homologies of Tetrapod Hindlimb Muscles, Comparison with Forelimb Muscles, and Deconstruction of the Forelimb-Hindlimb Serial Homology Hypothesis

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ABSTRACT

For more than two centuries, the idea that the forelimb and hindlimb are serially homologous structures has been accepted without serious question. This study presents the first detailed analysis of the evolution and homologies of all hindlimb muscles in representatives of each major tetrapod group and proposes a unifying nomenclature for these muscles. These data are compared with information obtained previously about the forelimb muscles of tetrapods and the muscles of other gnathostomes in order to address one of the most central and enigmatic questions in evolutionary and comparative anatomy: why are the pelvic and pectoral appendages of gnathostomes generally so similar to each other? An integrative analysis of the new myological data, combined with a review of recent paleontological, developmental, and genetic works and of older studies, does not support serial homology between the structures of these appendages. For instance, many of the strikingly similar forelimb and hindlimb muscles found in each major extant tetrapod taxon were acquired at different geological times and/or have different embryonic origins. These similar muscles are not serial homologues, but the result of evolutionary parallelism/convergence due to a complex interplay of ontogenetic, functional, topological, and phylogenetic constraints/factors. *Anat Rec*, 00:000–000, 2014. © 2014 Wiley Periodicals, Inc.

Key words: anatomy; evolution; homoplasy; limb muscles; phylogeny; serial homology; tetrapods

INTRODUCTION

The idea that the structures of the fore and hindlimbs (FL, HL) are serial homologues was first proposed by authors such as Vicq d'Azyr (1774), Oken (1843), and Owen (1849) and is still accepted in most textbooks and scientific articles. However, a careful examination of the original works of these authors reveals that their FL and HL comparisons were almost exclusively based on bones, and almost no attention was paid to soft tissues such as muscles, nerves, and blood vessels. Moreover, in

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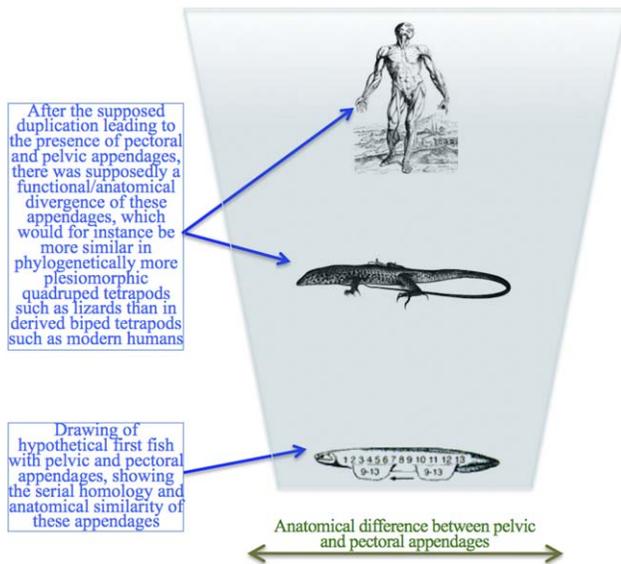


Fig. 1. Simplified diagram illustrating the “serial homology followed by functional/anatomical divergence” hypothesis often shown in textbooks and followed in more technical articles, particularly within the fields of developmental biology and evo-devo. The hypothetical fish is modified from Shubin et al.’s (1997) diagram showing the origin and evolution of paired appendages. According to that publication, establishment of serially homologous appendages resulted from gene co-option during the evolution of Paleozoic vertebrates. *Hox* genes were initially involved in specifying regional identities along the primary body axis, particularly in caudal segments. With the origin of gnathostomes, similar nested patterns of expression of *HoxD* genes were co-opted in the development of both sets of paired appendages (numbers shown within the fish body). According to this hypothesis, the co-option may have occurred in both appendages simultaneously, or *Hox* expression may have been initially present in PEL and then was co-opted in the development of an existing pectoral outgrowth (arrow below fish body; images of other taxa are modified from Diogo and Abdala, 2010 and references therein).

most cases the term “limb serial homology” clearly referred to what is currently viewed as evolutionary parallelism or convergence, i.e. homoplasy, as opposed to homology in the modern sense, i.e., common origin. True ancestral morphological or developmental serial homology of these appendages would imply that they are the result of an ancestral duplication; therefore, they must have been similar originally and only later diverged anatomically and functionally (Fig. 1).

The historical context of the FL-HL serial homology hypothesis was discussed in some detail by Diogo et al. (2013) and will be the subject of an extensive future work (in preparation). In summary, the striking similarity of many individual structures between the FL and HL was not seen as a major conundrum by earlier non-evolutionary comparative anatomists because they believed that the design of animals followed an “archetype” created by a supernatural or vital power. The romantic definition of “archetype,” which was partially followed by Owen, often referred to all possible phenotypes that a structure or organ could assume in development and evolution, similar to the current term “norm of reaction” (see, e.g., Russell, 1916; Richards, 2002). Therefore, within the *Naturphilosophie* paradigm followed by authors such as Oken, the term “serial

homology” did not necessarily imply anatomical duplication of a primitive “limb archetype.” This point is illustrated in *On the Nature of Limbs* (Owen, 1849), in which the examples of striking similarity between the FL and HL mainly include tetrapods with highly derived limbs such as bats, humans, horses, and plesiosaurs. Referring to these examples, Owen actually uses the word “parallelism” more often than “serial homology.” Moreover, when Owen discusses phylogenetically more plesiomorphic taxa such as chondrichthyans, he states that these taxa confuse the notion of “archetype” and “serial homology.” That is, his concept of “serial homology” referred to derived, particular cases of homoplasy, as opposed to the concept of serial homology that is commonly accepted today (see, e.g., Wagner, 1994; Roth, 1994; Wilmer, 2003; Diogo et al., 2013).

The similarity between the FL and HL was an important topic of discussion for early evolutionary comparative anatomists, who addressed the subject in two major ways (see, e.g., Humphry, 1872a,b; Quain et al., 1894; McMurrich, 1905; Bardeen, 1906; and references therein). Some followed the romantic idea that the vertebrate body is composed of a series of idealized, originally identical segments (e.g., Goodrich, 1930) and postulated that the HL is nothing more than a second FL, which was in turn often viewed as a derivative of a posterior branchial arch (e.g., Gegenbaur, 1878). Others argued that all hard and soft tissue structures present in the FL and HL of basal tetrapods were already present in some form in plesiomorphic gnathostome fish as the result of a unique, ancestral duplication of the paired appendages. An illustrative example is Humphry’s (1872b) argument that not only dipnoans but also fish such as sharks have “*latissimus dorsi*” and “*pectoralis*” muscles similar to those of extant tetrapods.

Since the publication of these classical studies, a large body of evidence has accumulated which contradicts the ideas that (1) the limbs are the result of supernatural or vital phenomena, (2) there is a perfect segmentation of the vertebrate body, and (3) muscles such as the *latissimus dorsi* or *pectoralis* were already present in early gnathostomes (e.g., Diogo and Abdala 2010; see paragraphs below). However, some authors continue to cite these and other classical studies to support the idea that the structures of the pectoral and pelvic appendages (PEC, PEL), including the tetrapod FL and HL, are serial homologues.

More recent developmental studies have contradicted Goodrich and Gegenbaur’s hypotheses about the origin of the paired appendages. These studies suggest that pectoral and pelvic fins actually evolved from continuous stripes of competency for appendage formation located ventrally and laterally along the embryonic flank (e.g., Don et al., 2012). In a continuation of this theory, the authors proposed that the paired appendages evolved with a shift in the zone of competency to the lateral plate mesoderm in conjunction with the establishment of the lateral somitic frontier, which allowed the formation of limb/fin buds with internal supporting skeletons (Don et al., 2012). The idea that the PEC and PEL are serial homologues is generally associated with the notion that these appendages were originally similar to each other, and that there was a subsequent functional/anatomical divergence between them (Diogo et al., 2013; Fig. 1). For instance, Don et al., (2012) explain that the ancestral

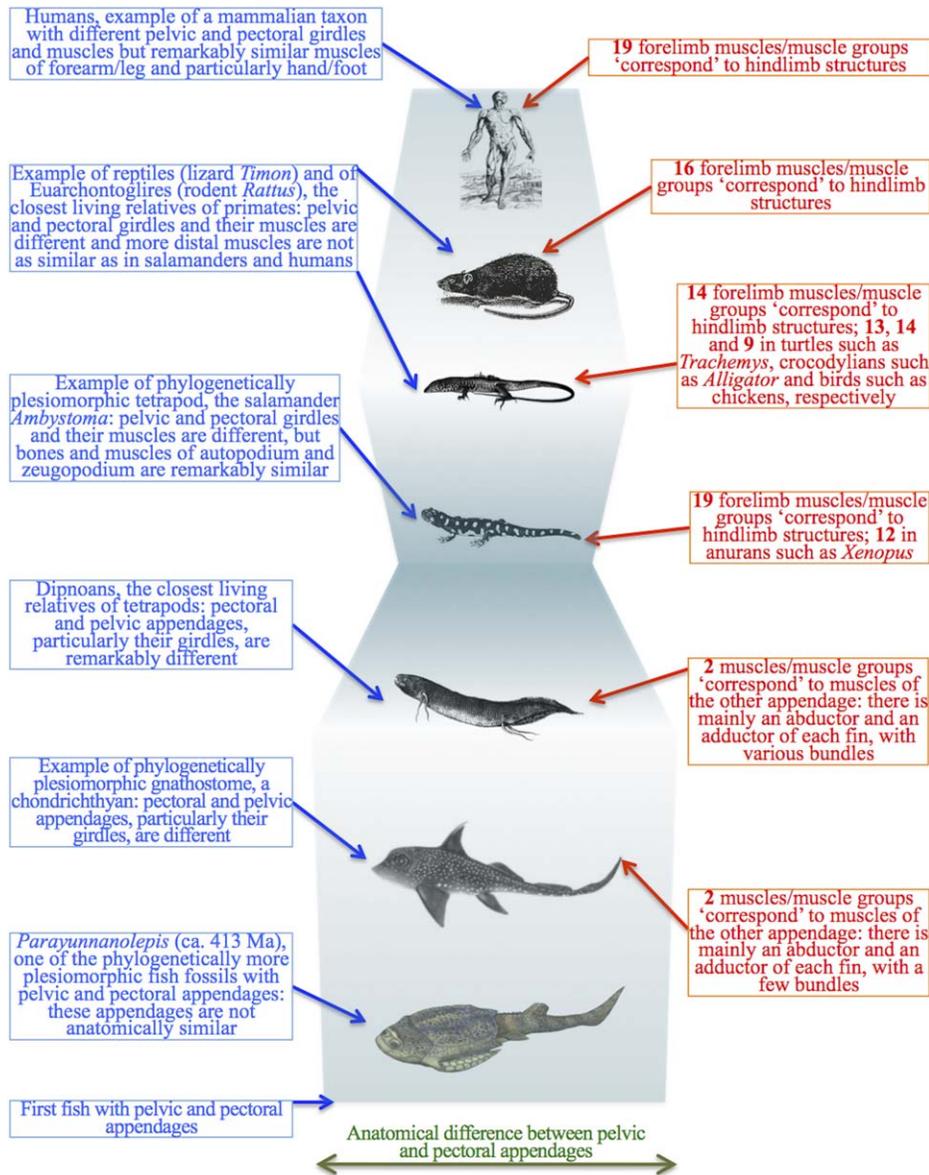


Fig. 2. Simplified diagram of the evolutionary transitions in muscle anatomy leading to modern humans (image of antiarch *Parayunnanolepis* modified from Zhu et al., 2012; images of other taxa modified from Diogo and Abdala, 2010 and references therein). The evolutionary history of the pelvic and pectoral appendages is much more complex

than the “serial homology followed by functional/anatomical divergence” hypothesis suggests. Complex interplay between ontogenetic, functional, topological and phylogenetic constraints leads to cases of anatomical divergence followed by convergence (“similarity bottlenecks”).

Tbx4/5 cluster in vertebrates probably underwent a duplication event, and now *Tbx4* is related to the HL and *Tbx5* to the FL of tetrapods; the authors then state that “pectoral fins evolved first and then duplicated to form pelvic fins” (see their Fig. 3). This example illustrates the common confusion in evo-devo studies between duplication of the *Tbx4/5* cluster and subsequent co-option of genetic pathways associated with the ontogeny of the different paired appendages, as opposed to the morphological duplication of the appendages themselves and their individual structures (e.g. muscles and bones). That similar genes contribute to an outgrowth that gives rise to different limbs in the same

animal does not necessarily mean that these limbs are serial homologues; similar genes and gene cascades/networks may have been simply recruited homoplastically as organizers of limb development (e.g., Wilmer, 2003).

Recent developmental, genetic, paleontological, and functional studies raise additional questions about the serial homology hypothesis. For example, a recent article on the most phylogenetically plesiomorphic fossil fish with PEC and PEL discovered so far (an antiarch placoderm) shows that these appendages are actually markedly different anatomically (Zhu et al., 2012; Fig. 2), supporting the idea that close similarity between the PEC and PEL in fish such as osteichthyans is a

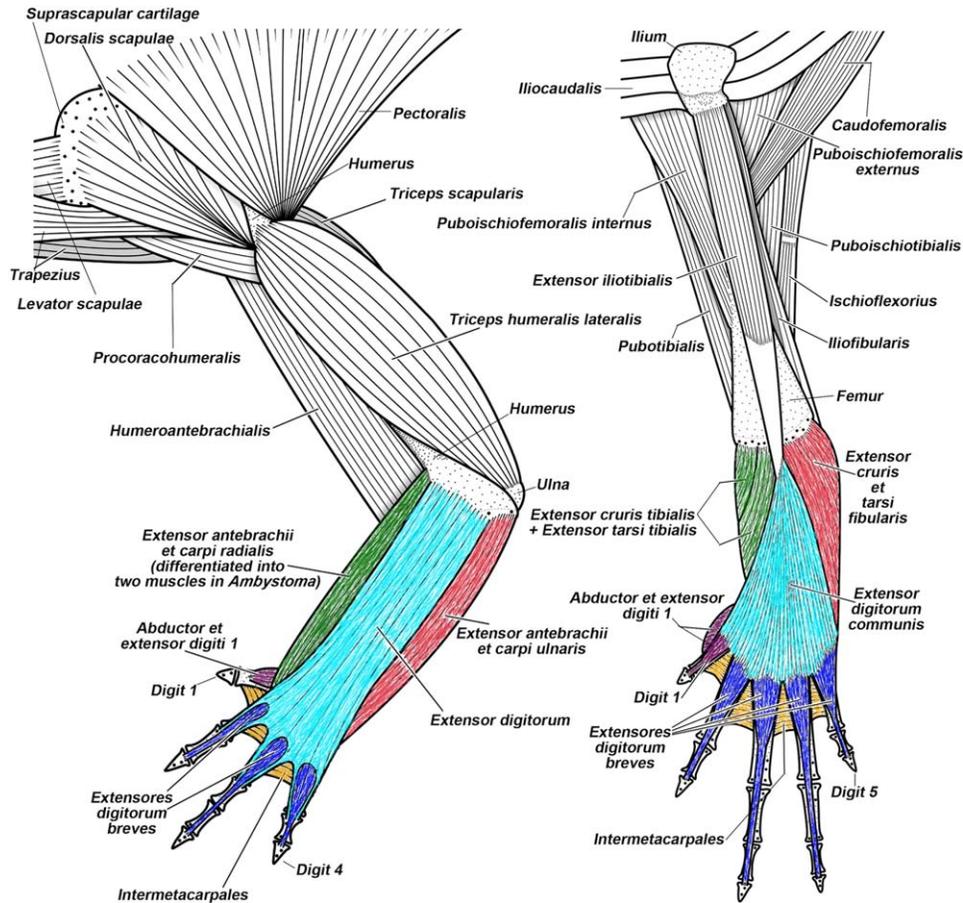


Fig. 3. Superficial musculature of the forelimb (on the left) and the hindlimb (on the right) of the salamander *Taricha torosa*, seen in dorsal view. Striking similarities between forearm-hand muscles and leg-foot muscles, as well as striking differences between the pectoral-arm muscles and the pelvic-thigh muscles, are evident in urodeles, includ-

ing this species and axolotls (modified from Diogo et al., 2013; N.B., because this figure shows a dorsal view and the original image shows a palmar/plantar—i.e., a ventral—view, there is no correspondence between the colors used in the two figures, i.e., they do not represent homologous structures between urodeles and modern humans).

specialized feature (e.g., Coates and Cohn, 1998). Moreover, recent functional studies have contradicted the old idea that the tetrapod FL and HL evolved in a terrestrial environment and originally had similar functions (e.g., Pierce et al., 2012). Developmental and genetic studies have demonstrated a surprisingly distinct lag between the developmental modes of pectoral and pelvic musculature, not only in fish but also in tetrapods (e.g., Cole et al., 2011; Piekarski and Olsson 2012; Don et al., 2012).

Careful review of the most detailed, and unfortunately often neglected, older developmental studies of the hard and soft tissues of the FL and HL in modern humans and other tetrapods also reveals major differences between the ontogeny of these tissues (e.g., Bardeen, 1906; Lewis, 1910; Cihak, 1972). For instance, Cihak (1972; p 142) stated that “a real homology of the two extremities (human FL and HL) is here hence invalid, the muscles, if corresponding by their function, are much more homodynamic structures.” According to Cihak, this statement also applies to skeletal tissues: “the (skeletal) primordia from various layers join in different mode in the hand and foot; it would be more

appropriate to speak of form accordances and similarities rather than of homologies (or serial homologies)” (see, Cihak, 1972; p 163).

An extensive review of these and other lines of evidence which contradict arguments often used to support the FL-HL serial homology hypothesis was recently published by Diogo et al. (2013). Based on that review, and on the results of a long-term study of the muscles of all major vertebrate groups by Diogo and colleagues (e.g., Diogo, 2007; Diogo and Abdala, 2007, 2010; Diogo and Wood, 2011, 2012; Diogo et al., 2008, 2009ab), Diogo et al. (2013) rejected the serial homology hypothesis. However, that project did not include extensive information about the hindlimb. This publication provides the first detailed information about the evolution and homologies of all HL muscles of representatives of each major tetrapod group, i.e., urodeles, anurans, turtles, lepidosaurs, crocodylians, birds, and mammals (Tables 1–12) and includes an updated summary of the evolution of the FL muscles of tetrapods. Therefore, this publication is the first to present detailed hypotheses concerning the evolution and homology of both FL and HL muscles of every major tetrapod group (Tables 13–21) and the culmination of a long-

TABLE 1. Scheme illustrating hypotheses regarding the homologies of the appendicular pelvic and thigh muscles of adults of representative tetrapod taxa (N.B., axial pelvic muscles such as the psoas minor and quadratus lumborum are not included in this table)

	<i>Timon lepidus</i> [15 pelvic and thigh muscles]	<i>Rattus norvegicus</i> [25 pelvic and thigh muscles]	<i>Homo sapiens</i> [25 pelvic and thigh muscles] ¹
Dorsal mass	Iliofemoralis	Gluteus medius (anterior & posterior heads)	Gluteus medius (has a single head)
	---	Piriformis	Piriformis
	---	Gluteus minimus (includes 'sarsorius' head) ^{3A}	Gluteus minimus
	---	---	---
	---	---	---
	---	Tensor fasciae latae	Tensor fasciae latae
	Extensor iliotibialis (Iliotibialis; anterior & posterior heads) ^{1A}	---	---
	---	---	---
	---	---	---
	---	---	---
Anterior	Tenuissimus (Iliofibularis) ^{3C}	Gluteus maximus	Gluteus maximus
	---	Rectus femoris ^{3D}	Rectus femoris
	---	---	---
	---	Vastus lateralis	Vastus lateralis
	---	Vastus intermedius ^{3F}	Vastus intermedius
	---	Vastus medialis	Vastus medialis
	---	---	---
	---	---	---
	---	---	---
	---	---	---
Adductors	Puboischiofemorale internus	Sartorius (3 heads) ^{3F}	Psoas major
	---	---	Iliacus
	---	---	Pectineus
	---	---	---
	---	---	---
	---	---	---
	---	---	---
	---	---	---
	---	---	---
	---	---	---
Hamstrings	Femorofibularis (see Table 3)	---	---
	Ischioflexorius (seems to include part/totality of fl.cr.ta.ti.) ^{1C}	---	---
	---	---	---
	---	---	---
	---	---	---
	---	---	---
	---	---	---
	---	---	---
	---	---	---
	---	---	---
Ischiotrochantericus	Puboischiofemorale externus	Quadratus femoris	Quadratus femoris
	---	Obturator internus	Obturator internus
	---	Gemellus superior	Gemellus superior
	---	Gemellus inferior	Gemellus inferior
	---	---	---
	---	---	---
	---	---	---
	---	---	---
	---	---	---
	---	---	---

Data compiled from evidence provided by dissections, comparisons and an extensive review of the literature. The black arrows indicate hypotheses that are most strongly supported by the evidence available; the grey arrows indicate alternative hypotheses that are supported by some data, but that overall are not as strongly supported by the evidence as are the hypotheses indicated by the black arrows. The muscles shown in bold are stressing the fact that the last common ancestor of tetrapods probably only had a muscle, at the maximum, that directly corresponds to an individual muscle present in modern humans, i.e. the gracilis. * indicates that the respective muscles have features of both anterior and posterior masses of dorsal mass, while # indicates that the respective muscles have features of both ventral and dorsal masses. ad., adductor; fl.cr.ta.ti, flexor cruris et tarsi tibialis; fl.tib.ext., flexor tibialis externus; g.m., gluteus maximus; te.fa.la., tensor fasciae latae.

TABLE 1. (Continued)

^{1A}Kardong (2002) states that the “ilioextensorius,” “part of puboischiofemoralis externus,” and “iliotibialis” of salamanders gave rise to, respectively, the femorotibialis, iliotibialis and “ambiens” of reptiles; however, as noted by Gadow (1882) and reported by Ashley-Ross (1992) and Walthall and Ashley-Ross (2006), in salamanders there is usually a single muscle extensor iliotibialis in this region (which however, often has anterior and posterior heads that are often named respectively as “iliotibialis” and “ilioextensorius” in urodeles: see, e.g., Appleton, 1928), which thus seems to correspond to the femorotibialis, iliotibialis and “ambiens” of lizards, as defended by authors such as Gadow (1882) and Walker (1954). The dissections and comparisons done for the present work of amphibians and reptiles strongly support this idea.

^{1B}At first sight, the “pubifemoralis” sensu Ashley-Ross (1992) could seem to correspond to the “ambiens” of reptiles and thus the sartorius of mammals, because in a dorsal view is just deep and anterior to the iliotibialis and at least partially deep to the puboischiofemoralis internus (e.g., Fig. 3A of Ashley-Ross, 1992), as is usually the “ambiens” of reptiles (e.g., Fig. 1.38 A of Russell and Bauer, 2008). However, reptiles may have both an “ambiens” and a “pubifemoralis,” although these muscles are often closely related and sometimes the two names are even used as synonyms (see, e.g., Russell and Bauer, 2008). The dissections and comparisons done for the present work clearly support the idea that the “pubifemoralis” of amphibians such as salamanders corresponds instead to the adductor femoris of reptiles such as lizards. This is because both the amphibian “pubofemoralis” and the reptilian adductor femoris are deep ventral muscles that lie just deep (dorsal) to the pubotibialis and that run from the ventral surface of the pelvic girdle to the ventral surface of the femur, while the reptilian “ambiens” is actually a dorsal muscle (see, e.g., Romer, 1942, and Jones, 1979). Moreover, if one compares the ventral pelvic/thigh muscles of reptiles such as lizards and amphibians such as salamanders, almost all homologies are straightforward and somewhat consensual, with two exceptions: the “pubifemoralis” and “ischiofemoralis” of amphibians and the adductor femoris and ischiotrochantericus of reptiles. Only a few authors have suggested that the amphibian “ischiofemoralis” might correspond to the adductor femoris (e.g., Gadow, 1882), most authors agreeing that it corresponds instead to the reptilian ischiotrochantericus, as defended here. For instance, Walker 1954 (p. 94) clearly defends this latter hypothesis, and states that the adductor femoris of *Necturus* is deeply blended with the puboischiofemoralis externus, as is precisely the case with the “pubofemoralis” (see e.g., Ashley-Ross, 1992; dissections done for the present work), thus supporting the two homologies defended in the present work. Kardong (2002; his Table 10.2) also states that salamanders have a muscle that is directly homologous to the adductor femoris of reptiles and that this muscle is topologically related with the pubotibialis, as is the amphibian “pubofemoralis”. Appleton (1928; p. 434) also states that the amphibian “ischiofemoralis” corresponds to the reptilian ischiotrochantericus and the “pubifemoralis”-adductor femoris synonymy was also defended by Francis (1934; p. 106). In fact, the dissections and comparisons done for the present work confirm that both these latter muscles are ventral muscles that originate mainly from the posterior portion of the pelvic girdle and that run mainly parallel to the girdle anteroposterior axis to attach onto the proximal region of the femur (compare, e.g., Fig. 1.38 of Russell and Bauer, 2008, to Fig. 6A of Ashley-Ross, 1992).

^{1C}As noted by authors such as McMurrich (1905) and Bardeen (1906) in urodeles such as *Ambystoma* the leg muscle flexor cruris et tarsi tibialis (sensu the present work) seems to correspond to the distal (leg) portion of the ischioflexorius. Most authors agree that the ischioflexorius of salamanders corresponds to both the flexor tibialis internus and flexor tibialis externus of lizards (e.g., Walker, 1954; Kardong, 2002) but some authors suggested that part of these two lizard muscles (e.g., of the flexor tibialis externus according to Gadow, 1882) might instead derive from more caudal musculature such as the caudalipuboischiotibialis (e.g., Gadow, 1882). This latter muscle is however, often regarded as part of the caudal-pelvic girdle musculature, although it should be noted that contrary to caudal-pelvic muscles such as the ischiocaudalis that connect the pelvis to the tail, the caudalipuboischiotibialis mainly connects the tail to the puboischiotibialis muscle, thus being probably related to flexion of the tail but also to limb retraction (e.g., Walthall and Ashley-Ross, 2006).

^{2A}Jones (1979) stated that authors such as Haines (1934) and Howell (1938) argued that the iliofemoralis and at least part of the iliotibialis of lizards correspond respectively to the deep and superficial gluteal muscles of mammals and that her embryological comparisons support this idea, because early in mice development the deep and superficial gluteal muscles are positioned respectively deep and superficial to the fibular nerve trunk, like the embryonic reptilian iliotibialis and iliofemoralis. The deep anlage in the mouse, i.e. the gluteus medius, gluteus minimus and piriformis, is clearly homologous to the lizard iliofemoralis because in both groups this anlage has an acetabular bony origin, a proximal insertion, and a position posterior to the fibular nerve trunk. Although some authors (e.g., Pearson, 1926) have homologized the piriformis with the ventrally derived reptilian muscle caudofemoralis, no embryonic association with ventral anlagen was ever noted in the mouse. The tensor fasciae latae appears to cleave from the anterior tip of the deep gluteal mass and become secondarily associated with the gluteus maximus. Although these features indicate that this muscle derives also from the iliofemoralis, an origin of this muscle from the superficial mass cannot be completely excluded as its differentiation closely follows the separation of deep and superficial gluteal layers.

^{2B}Jones 1979 stated that although the reptilian iliotibialis is difficult to homologize with mammalian muscles, it shares proximal features with the superficial gluteals and distal features with the rectus femoris in the adult condition (e.g., Romer 1922 and Appleton 1928). In early lizard ontogeny the iliotibialis anlage is a massive sheet of mesenchyme that originates from the acetabular region and covers the dorsal surface of the thigh superficial to the femoral nerve trunk. A similar condensation is found in embryonic E12 mice but in these embryos the cleavage divides this mass into anterior and posterior parts, the anterior part maintaining its acetabular origin and distal insertion and giving rise to the rectus femoris. The posterior part gives rise to the femoroccygeus and gluteus maximus. Both the anterior and posterior parts of the mammalian lateral mass and the reptilian anterior and posterior iliotibialis are also comparably positioned with respect to the femoral and fibular nerve trunks.

TABLE 1. (Continued)

^{2C}Jones (1979) argued that the tenuissimus of mammals is clearly homologous to the iliofibularis of reptiles, both muscles splitting off from the posterior dorsal mass of the pelvis/thigh very early in ontogeny, lying at the border of the dorsal and ventral masses postaxially, and innervated by a distal branch of the fibular nerve that separates them from the rest of the postaxial dorsal mass. The position of the tenuissimus deep to the biceps femoris in adult mammals has prompted doubt about this homology in the past but such a deep position is clearly derived because the tenuissimus of mice is superficial until embryonic stage E13.

^{2D}Jones (1979) stated that the lizard femorotibialis and mammalian vasti muscles are clearly homologous, both extending from the femur and being separated from more superficial extensors by the distal femoral nerve trunk; in fact some reptiles, e.g. chickens, have a femorotibialis divided into “externus,” “medialis” and “internus” heads that seem to correspond respectively to the vastus lateralis, intermedius and medialis of mammals, although these heads are deeply blended to each other and do not form separate muscles as in mammals (see, e.g., Schroeter and Tosney, 1991).

^{2E}The adult reptilian “ambiens” and the mammalian sartorius are quite different morphologically, especially with respect to their bony origins (Vaughn, 1956). However according to Jones 1979 the vestigial sartorius in mice shares several developmental features with the “ambiens” of lizards, e.g. both these muscles are derived from the preaxial dorsal mass, show a persistent proximal connection to the iliopsoas/puboischiofemoralis internus and lie anterodorsal to the femoral and saphenous nerves and vessels. The clear and early separation of the sartorius from the gluteals and quadriceps proximally and its lack of any association with the ventral musculature argue against homology with either the iliotibialis (e.g., Howell, 1938) or an adductor (e.g., Haines, 1934). The dissections and comparisons done for the present work clearly support the idea that the “ambiens” is homologous to the mammalian sartorius, because by applying a medial rotation of the femur in lizards as the one seeing during the ontogeny of mammals, the origin of the muscle becomes antero-proximo-lateral and the fibers of the muscle run distolaterally to a antero-disto-medial insertion, exactly as in mammals.

^{2F}Jones (1979) stated that in lizards the puboischiofemoralis internus derives from the anterior dorsal anlage, together with the “ambiens,” and corresponds to the iliopsoas (iliacus + psoas major) and the dorsal portion of the pectineus of mice, based on adult topology (Romer, 1922; Howell, 1938) and ontogeny. For instance, at early development both the mouse iliopsoas and the lizard puboischiofemoralis internus lie adjacent to the pubis and iliac acetabular regions and anterior to the femoral nerve trunk, insert laterally on the femur, and are connected distally to the anlage of the quadriceps/triceps group. At later stages the puboischiofemoralis internus of lizards migrates over the dorsal surface of the pubis and into the interior of the girdle, the iliopsoas of mice migrating anteriorly onto the iliac blade and trunk. The dorsal portion of the pectineus of mammals is often homologized with part of the puboischiofemoralis of lizards (e.g., Leche, 1883; Romer, 1922) and the embryonic derivation of the dorsal part of the pectineus from the anterior and proximal dorsal muscle mass in mice, opossums and humans. The ventral portion of the pectineus has been homologized with an adductor (e.g., Leche, 1883; Howell, 1938) or the pubotibialis (e.g., Vaughn, 1956) of reptiles and Jones’s ontogenetic comparisons support the idea that both the adductor longus and ventral portion of the pectineus of mammals correspond to the pubotibialis of lizards. This is because in lizard embryos the pubotibialis arises from the superficial anterior part of the ventral muscle mass and, according to her, homology of the ventral pectineus portion with the adductor femoris or puboischiofemoralis of lizards is excluded because of the position of the two latter muscles deep to the nerve to the gracilis. Further evidence that indicates a homology between part of the pubotibialis and the adductor longus include the identical positions of the two structures with respect to the branch of the obturator nerve to the gracilis and the origin of both structures from the anterior or adductor mass; one must assume that the tibial insertion was lost during the transition from reptiles to mammals. The dissections and comparisons done for the present work support the idea that the puboischiofemoralis internus gave rise to the pectineus, iliacus and psoas major, and actually one could hypothesize, based on the topology of its bundles, that parts 3, 2 and 1 correspond directly to part/the totality of the pectineus (the more posterior/medial in mammals), psoas major and iliacus (the more anterior/lateral in mammals).

^{2G}Jones (1979) stated that the adductor femoris in lizards is usually a stout mass that arises deep to the puboischiotibialis and is fused with the flexors on their inner surface, the “adductor brevis” (main body of adductor magnus sensu the present work) and adductor magnus (“adductor minimus” head of adductor magnus sensu the present work) developing in a similar position in the mouse. They arise initially as superficial extensions of the proximal anlagen and lie posterior to the major obturator trunk, the “adductor brevis” (main body of adductor magnus sensu the present work) having an insertion that extends further distally than that of the adductor femoris, but this develops very late in the mouse. However, because the adductor brevis of the mouse, sensu the present work, seemingly corresponds to either part of the “adductor longus” and/or of the “adductor magnus” sensu Jones (1979), it is not clear if the adductor brevis really derives from the adductor femoris or from the pubotibialis (the muscle giving rise to the adductor longus sensu Jones).

^{2H}Jones (1979) stated that the “puboischiotibialis” or lizards and the gracilis of mammals such as mice arise superficial to both the deep anterior part of the ventral muscle mass and the deep flexors, and are clearly homologous; both separate from the rest of the ventral mass early, have slips that migrate anteriorly during development, and are innervated by branches of the obturator that pierce homologous deep adductor muscles.

^{2I}Jones (1979) stated that the deep hamstring or flexor region of the ventral mass gives rise to the flexor tibialis internus complex in lizards, and to the ventral head of the semitendinosus, biceps and semimembranosus in mice. Apart from other clear similarities in ontogeny, both the flexor tibialis internus and the corresponding anlage in the mice divide early in development into two parts separated by a branch of the hamstring nerve, the more superficial part giving rise to the flexor tibialis internus 2 of lizards and to the biceps and ventral semitendinosus of mammals and being often blended to the caudofemoralis/dorsal semitendinosus of mammals and the caudifemorales/flexor tibialis externus of reptiles. The deeper portion gives rise to the flexor internus 1 of lizards and to the semimembranosus of mammals, and is often blended to the adductors in both mammals and reptiles.

TABLE 1. (Continued)

^{2J}Jones (1979) stated that because of its adult lateral position, the biceps femoris has frequently be confused with gluteal muscles (e.g., Greene 1935) or homologized with dorsally derived reptilian muscles (e.g., Gregory and Camp, 1918; Romer, 1922; Haines, 1935). However it clearly originates in mouse in association with the ventral musculature, migrating laterally or dorsally as ontogeny progresses. The mammalian semitendinosus is usually described as a single muscle with ventral (ischial) and dorsal heads of origin. Historically, however, the dorsal head has been treated separately and termed the “flexor cruris caput dorsale” (Appleton, 1928), the “caudal head of the biceps” (Cunningham, 1881), or the “crucrococcygeus” (Romer, 1942). When present the semitendinosus is distinguishable from the other hamstrings by its caudal superficial origin and its course dorsal to the caudofemoralis and the perinaealis and hamstring nerves. Its frequent large size and caudal origin led Romer (1922) to homologize the dorsal head of the semitendinosus with a part of the reptilian caudifemorales but its position with respect to nerves led Appleton (1928) to homologize it with the flexor tibialis externus. As the caudofemoralis and dorsal head of the semitendinosus are closely associated during ontogeny it is difficult to reject an origin from the reptilian caudifemorales or from the reptilian flexor tibialis externus. However, the posterior ontogenetic origin of the dorsal part of the semitendinosus and its extensive distal association with the other flexors suggest its homology with the flexor tibialis externus, because in early ontogeny both structures extend down the posterior surface of the thigh, later establishing more medial insertions on the shank. According to Bardeen 1906 in lizards the leg muscle flexor cruris et tarsi tibialis (sensu the present work) usually corresponds to the long distal tendon of the thigh muscle flexor tibialis externus, although it cannot be completely discarded that it also/instead corresponds to part of the leg muscle gastrocnemius internus, as proposed by McMurrich (1905).

^{2K}Jones (1979) stated that the proximal superficial hamstring region gives rise to the caudofemoralis and dorsal head of the semitendinosus in mammals, the caudifemorales and flexor tibialis externus in reptiles. Although the reptilian caudifemorales have been homologized with the mammalian caudofemoralis on the basis of similar relationships to nerves (Appleton, 1928), they form a large complex of muscles that extends from the tail region to the femur as the major retractors of the thigh. Further, the bulk of the reptilian caudifemorales inserts proximally, the mammalian caudofemoralis distally, and therefore some researchers suggested that the caudifemorales of reptiles correspond to caudal muscles (e.g., Haines, 1935) or instead to proximally inserting muscles such as the piriformis in mammals (e.g., Pearson, 1926). However, both the reptilian caudifemorales and the mammalian caudifemoralis form from the anterior part of the superficial hamstring mass, show medial connections to deep flexors and adductors at early stages, and are closely related ontogenetically with the ischiochanteric anlage. At intermediate and late stages, the reptilian caudifemorales expand, and their origin migrates dorsocaudally, while the mammalian caudofemoralis has an origin that migrates only slightly dorsally and an insertion that migrates distally.

^{2L}Jones (1979) stated that the mammalian obturator externus shares the following characteristics with the anterior portion of the puboischiofemoralis externus of reptiles: (1) an early posterior fusion with the ischiochanteric mass, (2) an anterior origin from the foramen and the pubis, and (3) an insertion early in development near the anteromedial trochanter. The anlage of the mammalian quadratus femoris is large and originating at early stages from the lateral surface of the ascending ramus of the ischium. This anlage is closely associated with the adductor magnus and obturator externus but shows only a very tenuous association with the caudofemoralis at early cleavage stages; these characteristics are very similar to those displayed by the posterior part of the reptilian puboischiofemoralis externus and support the homology of these two structures.

^{2M}Jones (1979) corroborated the homology between the mammalian obturator internus and gemelli and the reptilian ischiochantericus, for their are morphologically quite similar in the adult condition and share ontogenetic features such as an early association with the caudifemorales/caudofemoralis, an initial lateral bony origin that later migrates to the pelvic surface of the girdle, and a persistent connection to the deep adductors.

^{3A}According to Jones (1979) the scansorius is present in mouse E12 and E13 embryos, being developed from the anlage of the iliopsoas (not of the tensor fasciae latae/gluteal muscles) and then fusing with the gluteus minimus, which is thus divided at its origin by the passage of the nerve to the tensor fasciae latae into a gluteus minimus proper originating from the posterior part of the gluteal fossa and into a “scansorius” head originating from the lateral crest of the ilium and the iliac fossa.

^{3B}Also according to Jones (1979) the femorococcygeus can be recognized at E13.5 mice but is then integrated in the biceps femoris; the dissections of rats and mice done for the present work indicate that it probably corresponds to the anterior head of the biceps femoris of adult rats and mice.

^{3C}According to Greene (1935) in rats the biceps femoris has an anterior head that corresponds to the short head of humans originating from the last sacral and first caudal vertebrae with the caudofemoralis, a posterior head originating from the sciatic tuber anterior to the accessory head, and an accessory head originating from the sciatic tuber with the semimembranosus, the two latter heads forming the long head of the biceps of humans and all three heads attaching together onto the distal femur and proximal 2/3 of the tibia. However in the mice and rats dissected there is a biceps divided into the anterior head sensu Greene (1935) (which likely corresponds to the femorococcygeus, as suggested by Jones 1979 and by the fact that this head is innervated by the inferior gluteal nerve as reported by Greene, 1935) and a posterior head including the posterior and accessory heads sensu Greene (1935). It should be noted that authors such as Walker and Homberger (1997) refer to two heads as observed by us. A major problem with Greene’s (1935) hypothesis of homology between the long head of humans and the anterior head of rats is that the anterior head of rats crosses three joints (between axis and pelvis, pelvis and thigh and thigh and leg) while the short head of humans only crosses one joint (between the thigh and leg; N.B., both the posterior head of rats and the long head of humans cross two joints because they originate from the pelvis and insert onto the leg). In fact, the homology hypothesis of Greene (1935) was questioned by Jones (1979), who states that the mouse muscle tenuissimus that derives from the gluteal anlage and that in E18 lies on the distal portion of the femur disappearing later in ontogeny, corresponds to the short head of the biceps femoris of humans. The topology of the tenuissimus is effectively more similar to that of the short head of the biceps femoris of humans and the tenuissimus is innervated by the fibular nerve and the short head of humans is innervated by the common fibular division of the sciatic nerve. However, if Jones (1979) homology hypothesis is right it would mean that the short head actually derives from the gluteal anlage as does the tenuissimus of rats (and not from the hamstring anlage, as does the long head of the biceps femoris of humans).

TABLE 1. (Continued)

^{3D}Greene (1935) stated that in adult rats the rectus femoris has well-differentiated anterior and posterior heads but our dissections of rats and mice indicated that this muscle is mainly undivided, as reported by Walker and Homberger (1997).

^{3F}Distally some fibers of the vastus intermedius are somewhat distinct from those of its main body, so the former fibers may correspond to the ones that are sometimes considered to form the “articularis genus” of other mammalian taxa, which has a similar topology to the upper limb muscle anconeus of most mammals (which is however, seemingly a forearm muscle derived from the extensor carpi ulnaris) and to the posterior head of the triceps branchii of primates such as the strepsirrhines.

^{3G}Jones (1979) stated that in mice the sartorius is ontogenetically associated with, and perhaps a link between, the anterior dorsal mass (particularly the iliacus) and the posterior dorsal mass (particularly the quadriceps), and then disappears early in ontogeny (after E13; according to Greene (1935) in adult rats it is fused with the gluteus maximus and/or tensor fasciae latae), probably corresponding to the “ambiens” of reptiles and not to the structure that is sometimes designated as “sartotius” in for example, chickens.

^{3H}Jones (1979) also stated that in mice the dorsal portion of the pectineus derives from the anterior ventral anlage together with the iliacus and the psoas major while the ventral portion of the pectineus derives from the adductor anlage together with the adductor longus. According to her the double ontogenetic origin of the pectineus is “ancestral” although it is not clear if for rodents or for mammals as a whole.

^{3I}The “adductor brevis” sensu Greene (1935) corresponds to the “adductor magnus” of Jones (1979), because it is deep to (from a medial view, i.e. more lateral than) the “adductor magnus” sensu Greene (1935) (“adductor brevis” sensu Jones, 1979). However, the dissections of rats and particularly mice done for the present work clearly support a much more parsimonious hypothesis, i.e. that the muscles of these rodents are basically the same as seen in modern humans, i.e. particularly in mice the fleshy head that gave rise to the well-defined tendon of the adductor longus is thinner than is normally shown in illustrations of rats and mice, and just deep/posterior to the adductor longus there is a relatively well-separated structure that attaches onto the femur at about the same level as the adductor longus, just posterior to the attachment of this muscle. This structure is thus topologically very similar to the adductor brevis of modern humans, although it is thinner than the muscle of humans and a little bit more blended to the adductor magnus, and that is why it was probably not identified as a separate muscle in rats by Greene (1935), Walker and Homberger (1997), and Wingerd (1998) and also not identified in the mice embryos analysed by Jones (1979). Then, more posteriorly, lies the adductor magnus, which is also topologically similar to that of humans, including a main body (which corresponds to the “adductor brevis” of Jones, 1979, and to the “adductor magnus” sensu Greene, 1935) and an adductor minimus head (which corresponds to the “adductor magnus” of Jones, 1979, and to the “adductor brevis” sensu Greene, 1935) that is posterior and proximal to the main body of the muscle, exactly as it often happens in modern humans (see, e.g., plate 463 of Netter, 1989).

^{3J}Jones (1979) stated that a gracilis formed by a single head is the plesiomorphic condition for mammals, i.e. that the presence of two heads as in e.g. mice is a derived condition.

^{3K}According to Jones (1979) at E13 mice a slip connects the caudofemoralis and semimembranosus in the proximal thigh region and then appears to fuse with the semimembranosus, thus suggesting it is a presemimembranosus, and at E14 this presemimembranosus fuses dorsally with the caudofemoralis, and then later in ontogeny disappears. According to her the presemimembranosus is homologous to the hamstring (sciatic) part of the adductor magnus of humans and is present as a distinct muscle in other mammals, and the presence of both a caudofemoralis and a presemimembranosus is plesiomorphic according to her, this being a further case of parallelism between ontogeny and phylogeny.

^{3L}According to Jones (1979) during mouse ontogeny the posterior (her “ventral”) and anterior (her “dorsal”) heads of the semitendinosus have more affinity with the biceps femoris and the caudofemoralis, respectively, and the absence of the anterior (her “dorsal”) head in e.g. humans and of the posterior (her “ventral”) head in some rodents is a derived condition.

^{3M}The “cranial head of the semimembranosus” sensu authors such as Walker and Homberger (1997) corresponds to the caudofemoralis sensu Greene (1935), Jones (1979) and the present work.

⁴Apart from the major differences shown directly on the table, the major differences between adult humans and adult rats are (see, e.g., Greene, 1935): (1) the gluteus maximus of humans is innervated by the inferior gluteal nerve, while that of rats is by this nerve and also the inferior branch of the superior gluteal nerve; (2) in humans the piriformis and obturator internus are innervated by different nerves, but in rats there is a branch of the lumbo-sacral plexus that innervates both these muscles; (3) in humans the quadratus femoris is innervated by a special nerve from the sacral plexus, while in rats it is innervated by the posterior division of the femoral nerve; (4) in humans the psoas major and iliacus are innervated by L2 and L3 through the femoral nerve, while in rats these muscles are said to be innervated directly from L2 and L3 of the lumbar plexus; (5) the pectineus of humans is innervated by the femoral and obturator nerves, while in rats it is only by the femoral nerve; (6) in humans the adductor magnus is innervated by the sciatic and obturator nerves while in rats it is only by the obturator nerve; (7) in humans the long and short heads of the biceps femoris are respectively innervated by the tibial and fibular divisions of the sciatic nerve, while in rats the anterior head is by the inferior gluteal nerve and the posterior head (which corresponds to the posterior + accessory heads sensu Greene, 1935) is by the tibial division of sciatic nerve; (8) in humans the semitendinosus is by the tibial division of the sciatic nerve, while in rats the anterior (“principal”) head is by the tibial division of the sciatic nerve and the posterior (“accessory”) head is by a branch of the lumbo-sacral plexus.

TABLE 2. Scheme illustrating hypotheses regarding the homologies of the dorsal/extensor leg muscles of adults of representative tetrapod taxa (see caption of Table 1)

	<i>Ambystoma mexicanum</i> [9 dorsal/extensor leg muscles]	<i>Timon lepidus</i> [9 dorsal/extensor leg muscles]	<i>Rattus norvegicus</i> [9 dorsal/extensor leg muscles]	<i>Homo sapiens</i> [10 dorsal/extensor leg muscles]
	---	---	Extensor hallucis longus (d. 1)	Extensor hallucis longus (d. 1)
Long extensors	Extensor digitorum longus ('extensor digitorum communis'; m.I-V)	Extensor digitorum longus (m.II-III, not to digits)	Extensor digitorum longus (d. 2-5)	Extensor digitorum longus (d. 2-5)
	---	---	---	# Fibularis tertius (m.V)
	Extensor tarsi tibialis	Tibialis anterior	Tibialis anterior	? Tibialis anterior
	Extensor cruris tibialis	---	---	---
Extensor cruris et tarsi fibularis	Fibularis longus	Fibularis longus	Fibularis longus	Fibularis longus
---	Fibularis brevis	Fibularis brevis ^{3A}	Fibularis brevis	Fibularis brevis
---	---	---	---	---
Short extensors	---	---	Fibularis digiti quarti (m.IV in rats and d.4 in mice) ^{3A}	---
	---	---	Fibularis digiti quinti (m.V in rats and d.5 in mice) ^{3A}	---
	Extensores digitorum breves (4 muscles to d.2-5)	Extensores digitorum breves (4 muscles to d.2-5 + part short ex. d.1) ^{2A}	Extensor digitorum brevis (2 muscles to d.2-3) ^{3A} (but ex.ha.br. found in various non-primate mammals)	Extensor digitorum brevis (3 muscles to d.2-4)
---	---	---	Extensor hallucis brevis (d.1; short ex. d.1)	
Abductor et extensor digiti 1 (d.1; abductor + part short ex. d.1)	Abductor et extensor digiti 1 (d.1; abductor + part short ex. d.1) ^{3A}	---	---	

d., digits; ex., extensor; ex.ha.br., extensor hallucis brevis; m, metatarsals (attachments are in general only shown for muscles that often insert onto digits).

^{2A}In lizards such as *Timon* the abductor et extensor digit 1 seemingly includes both an abductor and part of the short extensor anlage to digit 1, the extensores digitorum breves including also part of the short extensor anlage to digit 1 and short extensors to digits 2, 3, 4 and 5. In mammals the short extensor to digit 1 is seemingly not fused to an abductor and often forms a distinct muscle extensor hallucis brevis, while the short extensors to the other digits might be included into the extensor digitorum brevis complex or instead also form distinct muscles (e.g. the fibularis digiti quarti to digit 4 and the fibularis digiti quinti to digit 5 in mice), or alternatively be missing (e.g. the short extensor to digit 5 seems to be missing in humans).

^{3A}Most authors consider that rats have no fibularis tertius, i.e. apart from the fibularis brevis and fibularis longus (which are present in humans) rats have only a fibularis digiti quinti and a fibularis digiti quarti. These two latter muscles are often considered to form a group with the fibularis longus and brevis, but according to authors such as Greene (1935) they are actually innervated by the deep fibular nerve, which innervates extensor hindlimb muscles such as the extensor digitorum brevis and does not innervate the fibularis longus and fibularis brevis (these muscles are innervated instead by the superficial fibular nerve). This fact, together with the fact that in rats the extensor indicis of the forelimb is very similar to the extensor digitorum brevis of the hindlimb because both these muscles go to digits 2 and 3, and that the extensor pollicis longus is very similar to the extensor hallucis longus because both these muscles go to digit 1, strongly suggests that in these rodents the fibularis digiti quarti and fibularis digiti quinti are actually the short extensors to digits 4 and 5 of the hindlimb, respectively, i.e. that they "correspond" to the extensor digiti quarti and extensor digiti quinti of the forelimb. This would imply that the fibularis digiti quinti and fibularis digiti quarti of rats lost the contact with the digital phalanges, because they insert respectively onto the distal ends of metatarsals 5 and 4. In fact, in the mice dissected by us and various other primates including primate taxa, the fibularis digiti quinti and/or fibularis digiti quarti do insert directly onto the extensor expansions of the digits, so for those cases one would not even need to explain any major change. So, this is clearly more parsimonious than accepting the following changes to contradict that the fibularis digiti quarti and fibularis digiti quinti are not short extensors of the digits, e.g. in rats: (1) the short extensor of digit 4 of the hindlimb would be lost; (2) the short extensor of digit 5 of the hindlimb would also be lost; while in the meanwhile two new muscles precisely going to digits 4 and 5 would be formed, i.e. (3) the fibularis digiti quarti would be formed from the lateral mass of leg muscles and (4) the fibularis digiti quinti would be formed from the lateral mass of leg muscles; and moreover (5) that the innervation of these two muscles, which should then be by the superficial fibular nerve (which innervates the lateral muscles of the leg) then was changed, the two muscles now being innervated by the deep fibular nerve that precisely innervates the short extensors of the leg/foot. Be that as it may, contrary to the "topological correspondence" in rats of the extensor indicis of the forelimb with the extensor digitorum brevis of the hindlimb (both muscles are clearly short extensors going to the phalanges of digits 2 and 3), the potential "correspondence" of the fibularis digiti quinti and fibularis digiti quarti of the hindlimb with the extensor digiti minimi and extensor digiti quarti of the forelimb in rats is a much less obvious one and can only be suggested after a much more extensive analysis of the data (including innervation, information about other muscles, etc.) because the two former muscles are clearly located in the lateral and not the extensor compartment of the leg and moreover do not go to the phalanges of the digits, as the extensor digiti minimi and extensor digiti quarti do, but instead to the metatarsals. Therefore, following the methodology outlined in the Materials and Methods of Diogo et al. (2013), these potential correspondences are not directly shown in Table 13. A different, but related question concerns the "correspondence" of the "fibularis tertius" of humans, which is innervated by the deep fibular nerve and goes to metatarsal V in humans, and thus could be seen as a remaining of the short extensor of the digit 5 of the hindlimb and thus of the fibularis digiti quinti of rats and thus to the extensor digiti minimi of the forelimb as suggested by Quain et al. (1894). However, there are three main points contradicting this idea: (1) lizards often have both a fibularis digiti quinti and a fibularis tertius indicating that these muscles cannot be homologous to each other; (2) humans have a short extensor to digit 5 in the foot, i.e. the part of the extensor digitorum brevis going to digit 5, and also have a fibularis tertius, indicating that these two structures cannot be homologous to each other (e.g., Russell and Bauer, 2008); (3) developmental studies indicate that the fibularis tertius actually derives from the anlage of the extensor digitorum longus, and not of the extensor digitorum brevis of the hindlimb (e.g., Lewis, 1910).

term comparative study of vertebrate musculature undertaken by the authors and colleagues.

MATERIALS AND METHODS

Tables 1 to 4 compare the HL muscles of the following key taxa, chosen from among the many tetrapod taxa

dissected by the author and colleagues (see below): the salamander *Ambystoma mexicanum*, the lizard *Timon lepidus*, the rodent *Rattus norvegicus*, and modern humans (*Homo sapiens*). The Norwegian rat was chosen because rats are often considered to be "anatomically generalized" therian mammals and because they are somewhat closely related to primates (both groups are

TABLE 3. Scheme illustrating hypotheses regarding the homologies of the ventral/flexor leg muscles of adults of representative tetrapod taxa (see caption of Table 1)

	<i>Ambystoma mexicanum</i> [6 ventral/flexor leg muscles]	<i>Timon lepidus</i> [6 ventral/flexor leg muscles]	<i>Rattus norvegicus</i> [7 ventral/flexor leg muscles]	<i>Homo sapiens</i> [8 ventral/flexor leg muscles]
	--- (fl.cr. ta.ti. seems included in ischioflexorius) ^{1A}	--- (fl.cr. ta.ti. seems included in fl.ti.ex. and eventually ga.in) ^{2A}	--- (fl.cr. ta.ti. seems included in ha.fa. and eventually ga.) ^{3A}	--- (fl.cr. ta.ti. seems included in ha.fa. and eventually ga.) ^{4A}
	---	Gastrocnemius internus (femorotibial)	Gastrocnemius (medial and lateral heads) ^{3A}	Gastrocnemius (medial and lateral heads) ^{4A}
	---	Gastrocnemius externus (femoral; sup. and deep heads)	Plantaris ^{3A}	Plantaris ^{4A}
	---	---	Soleus ^{3A}	Soleus ^{4A}
	Fl. dig. com. (d.1-5; includes fl.cr.ta.fi.) ^{1A}	Flexor digitorum longus (d. 1-5)	Flexor digitorum longus (d. 1-5)	Flexor digitorum longus (d. 2-5) ^{4A}
	---	---	---	Flexor hallucis longus (d. 1) ^{4A}
	Flexor accessorius medialis	--- ('flexor accessorius' is distal head of flexor digitorum longus) ^{2B}	Quadratus plantae (or derived instead from foot muscles?) ^{2B}	Quadratus plantae
	Flexor accessorius lateralis	---	---	---
	Contrahentium caput longum ^{1B}	---	---	---
	---	Popliteus ^{2C}	Popliteus	Popliteus ^{4A}
	Interosseus cruris	Interosseus cruris	---	---
	Tibialis posterior (pronator profundus)	Tibialis posterior (pronator profundus)	Tibialis posterior	Tibialis posterior ^{4A}

d., digits; fl.cr.ta.fi., flexor cruris tarsi fibularis; fl.cr.ta.ti., flexor cruris tarsi tibialis; fl.dig.com., flexor digitorum communis; fl.ti.ex., flexor tibialis externus; ga., gastrocnemius; ga.in., gastrocnemius internus; ha.fa., fascial insertion of hamstring muscles; sup., superficial.

^{1A}Most authors consider that the femorofibularis is a thigh muscle and that at least part of the gastrocnemius of reptiles derives from the flexor digitorum communis of plesiomorphic tetrapods. For instance it is often stated that the flexor digitorum communis of salamanders corresponds to both the gastrocnemius externus plus the flexor digitorum longus of lizards (p. 385 of Russell and Bauer, 2008). This is mainly the hypothesis followed in the present work. However, it cannot be discarded that the femorofibularis of salamanders is part of the flexor musculature of the leg, corresponding to part/totality of the extensor cruris et tarsi tibialis and/or extensor cruris et tarsi fibularis of the extensor musculature of the leg and thus to the gastrocnemius complex (internus and/or externus) of reptiles. In fact, Howell (1938) described a very similar muscle in birds, which he named “femorocruralis” and is innervated by the tibial nerve (and not by the obturator nerve as suggested by Gadow, 1882); as stressed by Howell (1938), this avian muscle seems to be the result of a proximal migration of part of the gastrocnemius complex, thus providing some support to the idea that the femorofibularis of amphibians might correspond to at least part of the gastrocnemius complex of reptiles. However, as noted by authors such as McMurrich (1905) and Bardeen (1906) in urodeles such as *Ambystoma* the leg muscle flexor cruris et tarsi tibialis (sensu the present work) actually seems to correspond to the distal (leg) portion of the ischioflexorius, and the flexor cruris et tarsi fibularis to the femoral head of the flexor digitorum communis. Thence the avian “femorocruralis” might well correspond to part/totality of the distal (leg) portion of the ischioflexorius that has migrated proximally. If this hypothesis is right, then the urodele configuration of the ventral muscles of the forearm is very similar to that of the ventral muscles of the leg, including the presence of a flexor antibrachii et carpi radialis/flexor cruris et tarsi tibialis anlage and of a flexor antibrachii et carpi ulnaris/flexor cruris et tarsi fibularis anlage, the main difference being that in the forearm the muscle/muscles derived from each anlage are present as distinct muscles, while in the leg they are fused with the thigh muscle ischioflexorius and with the leg muscle flexor digitorum communis, respectively. In summary, as explained above, we mainly follow here the consensual view that the femorofibularis is a thigh muscle, particularly because it is exclusively innervated by the sciatic nerve (e.g., Francis, 1934) and because there is no such muscle or any apparent derivative of it in the leg of anurans, strongly supporting the idea that this is actually a peculiar, derived thigh muscle of urodeles and not an important part of the tetrapod leg bodyplan that gave rise to amniote leg muscles. However, the hypothesis of Humphry (1872ab) that the femorofibularis might correspond to at least part of the short head of the biceps femoris of mammals such as humans cannot be completely discarded.

^{1B} As explained by authors such as McMurrich (1905), the contrahentium caput longum is seemingly completely absent in amniotes, although it cannot be discarded that part of it is fused with the flexor digitorum longus (or, much less likely, to deeper muscles such as the tibialis posterior/interosseus cruris).

^{2A} According to Bardeen (1906) in lizards the leg muscle flexor cruris et tarsi tibialis (sensu the present work) usually corresponds to the long distal tendon of the thigh muscle flexor tibialis externus, although it cannot be completely discarded that it also/instead corresponds to part of the leg muscle gastrocnemius internus, as proposed by McMurrich (1905).

^{2B} McMurrich (1905) and Ribbing (1909) named the distal head of the flexor digitorum longus of lizards and *Sphenodon* (sensu e.g. Russell and Bauer, 2008) as the “plantaris profundus accessorius 1” and the “flexor accessorius” respectively. McMurrich (1905) suggested that this structure derives from the “pronator profundus,” i.e. from the tibialis posterior sensu the present work. However, as Ribbing’s (1909) name indicates, the distal head of the flexor digitorum longus of lizards is actually very similar and seems to correspond to the flexor accessorius complex of amphibians, being mainly situated on the tarsal region and running distomedially to attach onto the plantar aponeurosis and/or the structures associated to it (see, e.g., Figs. 1.45 and 1.48 of Russell and Bauer, 2008). Ribbing (1938) also used the name “flexor accessorius lateralis” to designate the “tarsal part of the fibular head” of the flexor digitorum longus sensu Walker (1973). Houghton (1868) in turn used the name “flexori longus accessorius” to designate the distal part of the flexor digitorum longus of crocodylians such as alligators. That is, the flexor accessorius complex is a distinct structure in amphibians and seemingly corresponds to the distal bundle of the flexor digitorum longus of reptiles such as lizards, *Sphenodon* and turtles and crocodylians and to the distinct muscle quadratus plantae of mammals such monotremes and rats and humans. It is however, not clear if the last common ancestor of amphibians and amniotes had a flexor accessorius complex divided into medial and lateral parts, as is usually the case in urodeles and often the case in some mammalian taxa (e.g., Lewis, 1989), or present as a mainly undivided structure, as is usually the case in anurans and in turtles and squamates (where it is an undivided bundle of the flexor digitorum longus) and in mammals such as humans, for instance.

^{2C} Rewcastle’s (1977) proposition that the popliteus is derived from the anlage of the interosseus cruris, together with the fact that the in reptiles such as the lizard *Timon* the popliteus seemingly usually originates from the tibia only and not the femur, as well as to the indirect evidence that the forearm of lizards usually has a pronator accessorius that runs from the radius to the fibula, indicates that the popliteus actually derives from the interosseus cruris. In fact, according to Walker (1973) some turtles have “proximosuperficial” and “distodeep” portions of the interosseus cruris, which are apparently similar, respectively, to the popliteus and interosseus cruris of other reptiles such as lizards. Developmental studies of humans have also supported this hypothesis, because the popliteus does not derive from the gastrocnemius anlage but instead from a deeper anlage (e.g., Bardeen, 1906). Therefore, this shows a further example of homoplasy between the hind and forelimbs, because the mammalian pronator teres of the upper limb derives from the flexor antibrachii et carpi radialis anlage and not from the pronator quadratus anlage; actually, the pronator teres is a superficial muscle of the forearm in contrast to the pronator quadratus which is a very deep forearm muscle, while in the leg the popliteus is a very deep muscle. That is, in reptiles such as lizards the popliteus is ontogenetically more similar to the forelimb muscle pronator accessorius than to the forelimb muscle pronator teres.

TABLE 3. (Continued)

^{3A}Kardong's (2002) Table 10.2 states that the femorotibial or "internal" head of the gastrocnemius gave rise to the mammalian gastrocnemius medialis and flexor hallucis longus. However, it gave instead very likely rise to the mammalian gastrocnemius lateralis, soleus and plantaris. The dissections of mice and rats done for the present work support the idea that the soleus and plantaris derived from the lateral part of the gastrocnemius complex as proposed in developmental works such as that of Bardeen 1906, because topologically in rats these muscles lie, effectively, more laterally (on the fibular side) than in humans. According to Bardeen (1906) in mammals the leg muscle flexor cruris et tarsi tibialis (sensu the present work) usually corresponds to the fascial distal insertion of the thigh hamstring muscles, although it cannot be completely discarded that it also/instead corresponds to part of the leg muscle gastrocnemius, as proposed by McMurrich (1905).

^{3B}The dissections of mice and rats done for the present work show that the quadratus plantae of these mammals shares more similarities with the palmaris brevis of the hand than it does in humans, because the quadratus plantae of mice and rats also lies deep (less plantar) to the flexor digitorum brevis but is quite superficial and mainly lies on the fibular side of the foot (in humans the muscle is broader and less fibular), in the same way as the palmaris brevis lies mostly on the ulnar side of the hand. This could seem to indicate that, as the palmaris brevis of the hand derives from the flexores breves superficiales, the quadratus plantae could derive from the flexores breves superficiales group or from other foot muscles. However, it is commonly accepted that the quadratus plantae is instead a ventral (flexor) leg muscle that is closely related to the flexor digitorum/hallucis longus (e.g., Quain et al., 1894; McMurrich, 1905; Bardeen, 1906; Schaeffer, 1941). In fact, this muscle seems to correspond specifically to the ventral leg muscle complex formed by the flexor accessorius lateralis and flexor accessorius medialis of urodeles, because: (1) during human ontogeny, the quadratus plantae clearly starts to develop near the flexor digitorum/hallucis longus and then migrates distally, i.e. it is very likely a leg muscle that migrates to the foot (e.g., Bardeen, 1906; Cihak, 1972); (2) the flexor accessorius complex of plesiomorphic tetrapods such as urodeles mainly runs distomedially (to the tibial side) to insert onto the plantar aponeurosis formed by the flexor digitorum communis, and the quadratus plantae of mammals mainly runs distomedially to insert onto the tendons of the flexor digitorum longus, which derive from the flexor digitorum communis of amphibians; and (3) in amphibians such as urodeles the flexor accessorius complex is usually differentiated into a muscle flexor accessorius medialis and a muscle flexor accessorius lateralis, and the quadratus plantae of mammals, which is precisely often designated as "flexor accessorius" in the literature, is often differentiated into similar medial and lateral bundles/muscles (e.g., Lewis, 1989), so this might be a further case of parallelism in which there is a similar (homoplastic) differentiation of a same ancestral structure (the flexor accessorius complex) in different tetrapod clades (urodeles and some mammals).

^{4A}There is much confusion in the literature about the origin of the flexor digitorum longus, flexor hallucis longus and tibialis posterior of mammals, and interestingly this confusion is somewhat similar to the confusion concerning the flexor digitorum profundus and flexor hallucis longus of the upper limb, and also illustrates what is perhaps the most serious common problem in comparative myology: the tendency to consider homologous muscles of different animals as non-homologous, "special" muscles. Greene (1935) reports a "flexor hallucis longus"/"flexor fibularis" running from the fibula, interosseus membrane and tibia to the distal phalanx of digits 1–5, and a "flexor digitorum longus"/"flexor tibialis" running from the tibia and fibula to the terminal phalanx of digits 1–5 together (i.e. fused) with the tendons of the "flexor hallucis longus"/"flexor fibularis," which is designated "flexor hallucis longus" because it is more fibular than the "flexor digitorum longus," as in humans the belly of the flexor hallucis longus is more fibular than the belly of the flexor digitorum longus. However, contrary to humans, in rats and mice there is no distinct flexor hallucis longus going only to the hallux, i.e. the configuration of these two muscle structures is actually very similar to the heads of the flexor digitorum profundus of the rat forearm, which sends tendons to digits 1–5 of the hand, i.e. in rats there is no distinct flexor pollicis longus going to the hand only. Therefore, the two structures reported by Greene (1935) and most authors as two different muscles actually correspond to the fibular and tibial heads of the flexor digitorum longus sensu the present work; the dissections done for the present work confirmed that the fleshy bellies of these two heads were blended to each other as well. The homology of the tibialis posterior of mammals is actually also straightforward: in amphibians and reptiles there is a deep muscle "pronator profundus" that usually runs mainly distomedially from the fibula to the tibiale and/or metatarsal I. In phylogenetically plesiomorphic mammals such as marsupials the deep muscle tibialis posterior runs mainly distomedially from the fibula to the navicular tuberosity, which represents the tibiale of phylogenetically plesiomorphic tetrapods. The homology of the "pronator profundus" of non-mammalian tetrapods and of the tibialis posterior of mammals is thus clear, and was actually pointed out more than 14 decades ago by authors such as Owen 1866 (see also, e.g., Schaeffer, 1941). However, in more recent textbooks it is often stated that lizards and other reptiles do not have a tibialis posterior, and that the tibialis posterior of mammals corresponds to part of the gastrocnemius complex of lizards (e.g., Kardong, 2002, which is otherwise an excellent book). Also, authors such as Lewis (1989), who wrote a monograph that is also otherwise excellent, continue to accept the confusing statements of authors such as McMurrich (1905) and Bardeen (1906) that the flexor digitorum longus and the tibialis posterior are phylogenetically and ontogenetically more related to each other than to the flexor hallucis longus.

included in the clade Euarchontoglires). Tables 5 to 8 compare HL muscles of *Ambystoma* and the frog *Xenopus laevis*, while Tables 9 to 12 compare the turtle *Trachemys scripta*, the lizard *Timon*, the crocodilian *Alligator mississippiensis*, and the bird *Gallus gallus*. For more details about the choice of specific taxa, see Diogo and Abdala (2010) and Diogo et al. (2013).

Tables 13 to 21 summarize the "topological correspondences" between FL and HL muscles of all taxa, specifically the leg *vs.* forearm and foot *vs.* hand

(no apparent "topological correspondences" were found in the pelvic and thigh *vs.* pectoral and arm muscles: see Discussion). We opted to use the simplest, most conservative and thus least subjective method available to compare these muscles. This method, described in detail by Diogo et al. (2013), uses the historical criteria for "correspondence" between parts of an organism, i.e. "positional or topographical similarity" *sensu* Owen (1866) or "morphological congruence" *sensu* Shubin and Alberch (1986). Anatomical characteristics of each

TABLE 4. Scheme illustrating hypotheses regarding the homologies of the foot muscles of adults of representative tetrapod taxa (see caption of Table 1)

	<i>Ambystoma mexicanum</i> [32 muscles muscles]	<i>Timon lepidus</i> [25 foot muscles]	<i>Rattus norvegicus</i> [22 foot muscles]	<i>Homo sapiens</i> [19 foot muscles]
	Flexores breves superficiales (5 muscles to d.1-5)	Flexores breves superficiales (3 muscles to d.1-3)	Flexor digitorum brevis (d.2-4)	Flexor digitorum brevis (d.2-5)
	---	Lumbricales (2 muscles, to d.3-4)	Lumbricales (4 muscles, to d.2-4)	Lumbricales (4 muscles to d.2-4)
	Abductor digiti minimi (m.V)	Abductor digiti minimi (m.V)	Abductor digiti minimi (d.5)	Abductor digiti minimi (d.5)
	---	---	--- (<i>abductor hallucis</i> seemingly fused with flexor hallucis brevis)	Abductor hallucis (d.1)
	---	---	---	Interossei plantaris hallucis (d.1) ^{4A}
	Contrahentes pedis (5 muscles to d.1-5)	Contrahentes pedis (5 muscles to d.1-5)	Contrahentes pedis (2 muscles, to d.2,5) ^{3A}	---
	---	---	---	Adductor hallucis (oblique and transverse heads) ^{4A}
	---	---	Flexor digiti minimi brevis (= f.b.p. 10, to d.5)	Flexor digiti minimi brevis (= f.b.p. 10, to d.5) ^{4B}
	---	---	Flexor brevis profundus 2 (to fibular side of d.1) ^{3B}	Flexor brevis profundus 2 (fibular side of d.1)
	---	---	Flexor hallucis brevis (= f.b.p. 1, to tibial side of d.1) ^{3B}	Flexor hallucis brevis (= f.b.p. 1, tibial side of d.1)
	Flexores digitorum minimi (4 muscles to d.2-5)	---	---	---
	Interphalangei digiti 3 (1 muscle to d.3) ^{1A}	---	---	---
	Interphalangei digiti 4 (2 muscles to d.4) ^{1A}	---	---	---
	Flexores breves profundi (10 muscles to d.1-5)	Flexores breves profundi (10 muscles to d.1-5)	Flexores breves profundi (3,4,5,6,7,8,9, i.e. 7 muscles to d.2-5) ^{3B}	Interossei plantares (3 f.b.p. muscles to d.3,4,5)
	---	---	---	Interossei dorsales (4 f.b.p. muscles + 4 intern. = 4 muscles) ^{4C}
	Intermetatarsales (4 muscles connecting m.1-5)	Intermetatarsales (4 muscles connecting m.1-5)	Intermetatarsales (4 muscles connecting d.1-5) ^{3B}	---

d., digits; di., digitorum; f.b.p., flexores breves profundi; intern., intermetatarsales; m, metatarsales.

^{1A} It should be noted that recent studies of *Ambystoma mexicanum* (Diogo and Tanaka, 2012) confirmed that the members of this species usually have a muscle interphalangeus digiti 3 in the hand connecting the metacarpophalangeal and first interphalangeal joints of digit 3, as reported by, e.g., Grim and Carlson (1974). This muscle is very similar to the muscle interphalangeus digiti 3 of the foot, which connects the metatarsophalangeal and first interphalangeal joints of digit 3. The dissections and comparisons done for the present work revealed that, contrary to the hand, in the members of this species digit 4 of the foot has a similar muscle interphalangeus as well as a more distal muscle interphalangeus seemingly connecting the first and second interphalangeal joints of this digit.

^{3A} Greene (1935) described a single contrahens muscle in rats, from the contrahens fascia to the sesamoid bone of the fibular side of digit 2 (“adductor indicis”) but there is clearly also a contrahens from the contrahens fascia to the tibial side of digit 5 in the mice and rats dissected for the present work; many other rodents also have contrahentes to digits 2 and 5 of the foot (e.g., Rocha-Barbosa et al., 2007)

^{3B} Greene (1935) described interossei to digits 1 (1), 5 (1) and 2, 3 and 4 (2 each), in a total of 8 muscles; as he did in the descriptions of the hand muscles, he clearly confused the identity of these foot muscles, because as in the hand, our dissections of the foot indicate that rats have a full series of flexores breves profundi with 10 muscles in total, one to each side of each digit, and of intermetatarsales with four muscles in total, which mainly abduct the digits. All these muscles usually originate from the tarsal and/or metatarsal region, and the flexores breves profundi 1, 2 and 10 correspond to the “medial head of the flexor hallucis brevis,” “lateral head of flexor hallucis brevis” and “flexor digiti minimi brevis” sensu Greene (1935), the other 7 flexores breves profundi thus corresponding to part of the interossei sensu Greene (1935). Our dissections of mice and rats confirmed mice that the 10 flexores breves profundi and the four intermetatarsales are present as distinct muscles, i.e. more separated from each other than in humans, the axis, i.e. the digit having two intermetatarsales, being seemingly digit 4 as is the case of the foot of primates such as lemurs, not digit 2 as in the human foot.

^{4A} As explained by Diogo et al. (2012), in the human foot the adductor pollicis accessorius (“volaris primus of Henle”: Diogo et al., 2012; Bello-Hellegouarch et al., 2012) is mirrored by the “interossei plantaris hallucis” sensu Cihak (1972), which as the “volaris primus of Henle” is probably derived from the contrahentes layer and namely from the adductor hallucis in this specific case, but could alternatively be derived from the flexores breves profundi layer. It should also be noted that both the transverse and oblique heads of the adductor pollicis are mainly derived ontogenetically from the anlage of contrahens 1, while in the foot the oblique head of the adductor hallucis is derived from the anlage of contrahens 1 but the transverse head is derived from a different, neomorphic anlage of the contrahens layer (e.g. Cihak, 1972); this is a further example of homoplasy/parallelism between the hand and foot muscles.

^{4B} According to the developmental study of Cihak (1972), contrary to the opponens hallucis (which is absent at all stages of normal human ontogeny, although may be present as anomaly/variation in some humans), the opponens digiti minimi of the foot is always present as a distinct structure in early normal human ontogeny, just next to the flexor digiti minimi brevis, but later becomes unrecognizable as a distinct structure.

^{4C} As also explained by Cihak (1972), as some dorsal interossei of the human hand seemingly include part of the dorsometacarpals, which are originally part of the dorsal/extensor muscles of the forearm, some dorsal interossei of the human foot seemingly also include part of the dorsometacarpals, which are originally part of the dorsal/extensor muscles of the leg (the dorsometacarpals are present as distinct muscles in adults of tetrapod taxa such as the Anura, for instance). The muscles shown in bold are stressing the fact that the last common ancestor of tetrapods probably only had a muscle, at the maximum, that directly corresponds to an individual muscle present in modern humans, i.e. the adductor digiti minimi.

muscle (distal attachments, proximal attachments, number of divisions, relations to other hard and soft-tissue structures, orientation of fibers, and number of joints crossed) were analyzed to determine which HL muscles shown in Tables 1 to 12 have clear, direct (one to one) “topological equivalents” in the FL of the same taxa (Tables 13–21). This method also allows meaningful comparison between taxa, the results of which are given in Tables 13 to 21, including new information about the evolution and homologies of all HL muscles in the taxa

shown in Tables 1 to 12. Nontopological data, which could suggest more “speculative/overdone” and/or “obscure/less apparent” cases of “correspondence” (e.g. ontogeny of wildtype animals, development of transgenic animals, gene expression) are discussed in relevant sections of the text and in other tables. For more details about the methodology and illustrative examples of how it was applied, see Diogo et al. (2013).

Figure 3 shows an example of the striking topological similarity between some muscles of the forearm-hand and

TABLE 5. Scheme illustrating hypotheses regarding the homologies of the appendicular pelvic and thigh muscles of adults of representative urodele and anuran amphibian taxa (see caption of Table 1)

		<i>Ambystoma mexicanum</i> [12 pelvic and thigh muscles]	<i>Xenopus laevis</i> [17 pelvic and thigh muscles] ^{2D}
Dorsal mass	Posterior	Iliofemoralis	Iliofemoralis
		Tenuissimus ('iliofibularis')	Tenuissimus ('iliofibularis')
Anterior	Adductors	Extensor iliobtibialis ('iliotibialis'; anterior & posterior heads)	Extensor iliobtibialis A ('tensor fasciae latae')
		---	Extensor iliobtibialis B (' gluteus maximus ') Cruralis
Ventral mass	Hamstrings	Puboischiofemoralis internus	Puboischiofemoralis internus A ('iliacus internus')
		---	Puboischiofemoralis internus B ('iliacus externus'; 3 heads)
Ischiotrochantericus	Hamstrings	Adductor femoris ('pubofemoralis')	Adductor femoris (' adductor magnus '; 2 heads) ^{2A}
		---	--- (but pubotibialis B, i.e. 'semitendinosus', present in other anurans) ^{2A}
Ischiotrochantericus	Hamstrings	Pubotibialis	Pubotibialis A ('sartorius'; 2 heads) ^{2A}
		Gracilis ('puboischiotibialis', proximal & distal heads)	Gracilis major ^{2B} Gracilis minor ^{2B}
Ischiotrochantericus	Hamstrings	Ischioflexorius (seems to include part/totality of fl.cr.ta.ti.)	Ischioflexorius (' semimembranosus '; 2 heads; fl.cr.ta.ti. seems to correspond to <i>crurostragalus</i>) ^{2B}
		Femorofibularis	---
Ischiotrochantericus	Hamstrings	Caudofemoralis	Caudofemoralis ('piriformis'; may be reduced or absent in some <i>Xenopus</i> specimens)
		Puboischiofemoralis externus	Puboischiofemoralis externus A ('pectineus')
Ischiotrochantericus	Hamstrings	---	--- (but puboischiofemoralis externus B, i.e. 'adductor longus', present in other anurans)
		Ischiotrochantericus ('ischiofemoralis')	Ischiotrochantericus A (' gemellus ') ^{2C}
Ischiotrochantericus	Hamstrings	---	Ischiotrochantericus B ('obturator externus') ^{2C}
		---	--- (but ischiotrochantericus C, i.e. 'quadratus femoris', present in other anurans) ^{2C}
Ischiotrochantericus	Hamstrings	---	Ischiotrochantericus D (' obturator internus ') ^{2C}

The muscles that are usually named “tensor fasciae latae,” “gluteus maximus,” “gemellus,” “obturator externus,” “quadratus femoris,” “obturator internus,” “pectineus,” “adductor longus,” “iliacus,” “sartorius,” “semitendinosus,” and “adductor magnus” in anurans are clearly not homologous to the muscles designated with the same name in humans, because the last common ancestor of amphibians and amniotes did not have any of these muscles, thence we use a different name in anurans. There are however, a few cases (highlighted in bold) in which although the muscle that is designated with a certain name in anurans does not directly correspond to the muscle designated with the same name in humans, both the anuran and human muscles derive from a similar anlage/ancestral muscle: the anuran “gluteus maximus” and the human gluteus maximus derive from the extensor iliobtibialis, the anuran “adductor magnus” and the human adductor magnus derive from the adductor femoris, the anuran gracilis major and gracilis minor and the human gracilis derive from the gracilis, the anuran “semimembranosus” and the human semimembranosus derive from the ischioflexorius, and the anuran “gemellus” and “obturator internus” and the human gemelli and obturator internus derive from the ischiotrochantericus. We prefer to use A, B, C and D to designate the anuran muscles, instead of I, II, III and IV, because names such as “puboischiofemoralis I” or “puboischiofemoralis internus II” are often used to designate the heads of the muscle puboischiofemoralis internus of lizards. fl.cr.ta.ti, flexor cruris et tarsi tibialis.

^{2A}The “adductor magnus” of anurans clearly seems to correspond to the adductor femoris (i.e., the “pubofemoralis”) of salamanders, although the hypothesis of Noble (1922) that it also receives a contribution from the pubotibialis of salamanders cannot be completely discarded.

^{2B}The present work follows Prikryl et al.’s (2009) idea that the anuran gracilis major and minor seem to correspond to the gracilis of urodeles but also Noble’s (1922) idea that the anuran “semimembranosus” mainly seems to correspond to the ischioflexorius of urodeles, and namely to its proximal (thigh) portion (the distal portion of the ischioflexorius of urodeles seemingly corresponds to the flexor cruris et tarsi tibialis: see Tables 1 and 7). Prikryl et al. (2009) suggested that the anuran “semimembranosus” derived from the urodele gracilis, but then in their text and their Table 2 they do not explain to which anuran muscle/muscles corresponds the urodele ischioflexorius. They also seem to have forgotten/neglected the urodele pubofemoralis in their Table 2 because they do not list that muscle, which is also clearly part of the bauplan of urodeles as can be seen in their own figures and descriptions of these amphibians. However, the hypothesis of Noble (1922) that the anuran gracilis major and minor might also receive a contribution from the ischioflexorius and the hypothesis of Prikryl et al. (2009) that the “anuran” semimembranosus might receive a contribution from the gracilis of salamanders cannot be completely discarded.

^{2C}The present work follows Prikryl et al.’s (2009) idea that the ischiotrochantericus of axolotls correspond to the “quadratus femoris,” “gemellus” and “obturator externus” of anurans, and possibly also to the “obturator internus” of anurans as proposed by Noble (1922).

^{2D}In general, the ontogenetic study of Dunlap (1966) supports the hypothesis of homology and evolution of the anuran pelvic and thigh muscles shown in this Table, with two major exceptions: the “tensor fasciae latae” shares an anlage with the “pectineus” and “abductor longus” and not with the cruralis and “gluteus maximus,” and the “adductor magnus” develops from the anlage that gives rise to the “gemellus,” “obturator externus,” “quadratus femoris” and “obturator internus”.

the leg-foot of salamanders. Nomenclature for the FL muscles follows Diogo and Abdala (2010) and Diogo and Tanaka (2012), and that of the HL muscles follows Diogo et al. (2010). In these and other previous publications, Diogo et al. proposed a unifying muscle nomenclature for the clade Tetrapoda and vertebrates as a whole which takes into account the nomenclatures used in human anatomy (e.g., Terminologia Anatomica 1998) and anatomy of other vertebrates (e.g., Nomina Anatomica Veterinaria

2005). Following this nomenclature, homologous muscles of the *same limb in different taxa* in Tables 1 to 21 are always designated by the same name. Other commonly used names are also given to facilitate comparison with articles by other authors. In addition to the taxa listed in Tables 1 to 21, Diogo et al. have dissected hundreds of specimens from all major groups of vertebrates (Diogo and Abdala, 2010; Diogo and Wood, 2012), and these results provide a comparative context for the Discussion.

TABLE 6. Scheme illustrating hypotheses regarding the homologies of the dorsal/extensor leg muscles of adults of representative urodele and anuran amphibian taxa (see caption of Table 1)

	<i>Ambystoma mexicanum</i> [9 dorsal/extensor leg muscles]	<i>Xenopus laevis</i> [16 dorsal/extensor leg muscles]
Long extensors	Extensor digitorum longus ('extensor digitorum communis'; m.I-V)	Extensor digitorum longus (to extensores digitorum breves of digits 3 and 4)
	---	^{2A} Tarsalis anticus
	Extensor tarsi tibialis	Tibialis anticus brevis ^{2A}
	Extensor cruris tibialis	Extensor cruris tibialis ('extensor cruris brevis') ^{2A}
	Extensor cruris et tarsi fibularis	Peroneus ^{2A}
Short ext.	---	Tibialis anticus longus ^{2A}
	---	Dorsometarsales ('extensores breves profundi'; 5 muscles to d.1-5) ^{2B}
	Extensores digitorum breves (4 muscles to d.2-5)	Extensores digitorum breves ('e.b.s.+e.b.m.'; 4 muscles to d.1-4) ^{2B}
	Abductor et extensor digiti 1 (d.1; abductor + part short extensor d.1)	Abductor brevis dorsalis hallucis (m.I)

As can be seen in the names highlighted in bold there are some cases in which, although the muscle that is designated with a certain name in anurans does not directly correspond to the muscle designated with a similar name in humans (but not the same, thence we can use the commonly used anuran names), both the anuran and human muscles derive from a similar anlage/ancestral muscle: the anuran “tibialis anticus brevis” and the human tibialis anterior (anticus) derive from the extensor tarsi tibialis, and the anuran “peroneus” and the human fibularis (peroneus) longus/brevis derive from the extensor cruris et tarsi fibularis (N.B., regarding the extensor digitorum longus and the extensores digitorum breves of anurans, they mainly correspond directly to the extensor digitorum longus and extensor digitorum brevis of humans, because they were present in the last common ancestor of tetrapods). d., digits; “ext., extensors; e.b.s.+e.b.m.+e.b.p., “extensores breves superficiales” plus” extensores breves medii” sensu Dunlap, 1960; m., metatarsals.

^{2A} The peroneus of anurans clearly seems to correspond to part or the totality of the extensor cruris et tarsi fibularis of urodeles, as this muscle lies on the fibular side of the dorsal leg and inserts on the fibularis. Regarding the tibialis anticus longus, the name might suggest that it corresponds to part of the extensor cruris et tarsi tibialis anlage and not of the extensor cruris et tarsi fibularis anlage as proposed in the present work. However, the hypothesis defended in the present work is actually supported by both topological and ontogenetic evidence because the tibialis anticus longus lies mainly on the fibular side of the leg and is usually partially inserted onto the fibulare and fused with the peroneus, and moreover seems to develop together with the peroneus from a same anlage (Dunlap, 1966). In fact, some authors refer to the tibialis anticus longus as a head of the peroneus (see, e.g., Ecker, 1864). If the tibialis anticus longus and peroneus of frogs effectively derive from a same (fibular) anlage, then they are somewhat similar to the fibularis brevis and fibularis longus of amniotes, although it is not clear if this is due to a parallelism or instead to a true homology, i.e. if the last common ancestor of tetrapods already had these two separated muscles. As noted by Dunlap (1960) and Dunlap (1966) the tibialis anticus brevis and tarsalis anticus seemingly derive from the same anlage (together with the extensor digitorum communis) and in some anurans the configuration and attachments of these two muscles thus supporting the idea that they derive from a same muscle mass.

^{2B} The “extensores breves profundi” sensu Dunlap (1960) clearly derive from the extensores digitorum breves, because they are the ones that send tendons to the distal phalanges of the digits, as do the extensores digitorum breves of the hindlimb and of the forelimb of urodeles. However, contrary to urodeles, in anurans the “extensores breves profundi” are separate, distinct muscles, as reported by e.g. Dunlap (1960), thus constituting the dorsometatarsales series of muscle sensu the present work, as the “extensores breves profundi” of the anuran forelimb constitute the dorsometacarpales series. The abductor brevis dorsalis hallucis clearly corresponds to the abductor part of the abductor et extensor digit 1 of urodeles, but as noted by Dunlap (1960) it is usually present as a distinct muscle in anurans although in some taxa it might be deeply blended with the extensor digiti brevis 1 or even be missing as a distinct muscle.

RESULTS

Homologies and evolution of tetrapod HL muscles are mainly presented in Tables 1 to 12, while topological similarities between tetrapod FL and HL muscles are presented in Tables 13 to 21. We observed some remarkable cases of topological similarity between the FL and HL muscles in specific tetrapod taxa, which are discussed below.

Table 13 shows a notable example of FL-HL integration due to homoplasy: in rats, the short extensors of digits 2 and 3 are fused to form an undivided muscle in both pairs of limbs, i.e., extensor indicis in the FL and extensor digitorum brevis in the HL. As shown in Table 13, these fusions, and the resulting similarity between the HL extensor digitorum brevis and the FL extensor indicis in rats, were clearly acquired independently in each limb and constitute an example of evolutionary parallelism/convergence (as opposed to serial homology) between the FL and HL.

Table 14 shows two further examples of FL-HL homoplasy. The HL muscle popliteus and the FL muscle

pronator teres of mammals are often said to “topologically correspond” to each other (e.g., Quain et al., 1894; Diogo et al., 2013). However, the popliteus derives evolutionarily from the interosseus cruris and is very similar, topologically, to the pronator accessorius of the forearm of lizards (Table 14). The FL muscle flexor carpi radialis and the HL muscle tibialis posterior are also said to be “topological equivalents” (e.g., Quain et al., 1894; Diogo et al., 2013). However, the tibialis posterior actually corresponds to a deep leg muscle in amphibians and reptiles often designated “pronator profundus”, which is ontogenetically and topologically similar to the palmaris profundus 1 of the FL in adult amphibians (Table 14). In both cases, “topological correspondence” between a certain HL muscle and a certain FL muscle in phylogenetically more plesiomorphic taxa becomes less perceptible in more derived taxa; however, in the latter taxa there is an apparent “topological correspondence” between the original HL muscle and a different FL muscle. The muscles tibialis posterior and

TABLE 7. Scheme illustrating hypotheses regarding the homologies of the ventral/flexor leg muscles of adults of representative urodele and anuran amphibian taxa (see caption of Table 1)

	<i>Ambystoma mexicanum</i> [6 ventral/flexor leg muscles]	<i>Xenopus laevis</i> [6 ventral/flexor leg muscles]
Long flexors	Flexor digitorum communis (d.1-5; includes fl.cr.ta.fi.)	Flexor digitorum communis (plantaris longus ; directly only to d.1-2) ^{2A}
	--- (fl.cr.ta.fi. seems to be included in ischioflexorius)	Cruroastragalus ('tibialis posticus'; seems to correspond to fl.cr.ta.fi.) ^{2A}
	Flexor accessorius medialis	Flexor accessorius ('transversus plantae proximalis et distalis') ^{2A}
	Flexor accessorius lateralis	---
	Contrahentium caput longum	Contrahentium caput longum ('tarsalis posticus'; derived also/instead from f.b.s?) ^{2A}
	Interosseus cruris	Interosseus cruris ('intertarsalis') ^{2A}
	Tibialis posterior ('pronator profundus')	Tibialis posterior ('plantaris profundus'; or 'palmaris profundus' derived instead from f.b.s?) ^{2A}

As can be seen in the names highlighted in bold there are some cases in which, although the muscle that is designated with a certain name in anurans does not directly correspond to the muscle designated with a similar name in humans, both the anuran and human muscles derive from a similar anlage/ancestral muscle: the anuran *plantaris longus* and the human *plantaris* derive from the flexor digitorum communis (N.B., the anuran “tibialis posticus” and the human tibialis posterior do not seem to be homologous, as shown in this Table). d., digits; f.b.s., flexores breves superficiales; fl.cr.ta.fi., flexor cruris et tarsi fibularis; fl.cr.ta.ti., flexor cruris et tarsi tibialis.

^{2A} The presence of a single leg bone (cruris) and the remarkable proximodistal elongation of the tibiale and fibulare bones in anurans seems to have led to a functional convergence between these bones and the tibia and fibula of tetrapods such as urodeles. An illustrative example supporting this idea is the fact that the “intertarsalis” muscle of anurans, which clearly seems to correspond mainly to the interosseus cruris of urodeles, fills the space between the tibiale and the fibulare, while in urodeles it fills the space between the tibia and fibula. Another example is that the anuran “tarsalis posticus” probably corresponds to the contrahentium caput longum of urodeles, because the anuran muscle is ventral (superficial) to the “intertarsalis” and develops from the same anlage that gives rise to intertarsalis (Dunlap, 1966). Dunlap (1966) stated that this anlage is closely related to the anlage of the flexores breves superficiales and gives rise to the “plantaris profundus”. Authors such as Gaupp (1896) and Perrin (1892) suggested that the “plantaris profundus” probably corresponds to the most tibial part of the flexores breves superficiales of urodeles because: 1) it is a relatively superficial, tibial muscle that is related to the plantar aponeurosis, which normally sends tendons to digits 1 and 2 in anurans; 2) in anurans there are usually no separate flexores breves superficiales to the foot digits 1 and 2 (e.g., Dunlap, 1960); and 3) in anurans, and particularly in the most plesiomorphic anuran taxa, the plantaris profundus is deeply fused with the flexores breves superficiales (e.g., Dunlap, 1960). However, the dissections and comparisons done for the present work, as well as the ontogenetic data published by Dunlap (1966), indicate that the “plantaris profundus” of anurans actually corresponds to the “pronator profundus” of urodeles, i.e. to the tibialis posterior sensu the present work. This is because: 1) Dunlap (1966) stated that in anurans the “tarsalis posticus,” the “intertarsalis” and the “plantaris profundus” derive from the same ontogenetic anlage, as normally do the interosseus cruris and the “pronator profundus” (i.e., the tibialis posterior), which are closely related to the contrahentium caput longum; 2) in adult anurans the “tarsalis posticus,” the “intertarsalis” and the “plantaris profundus” are also topologically associated because they all lie on the tarsal region, as does the “transversus plantae proximalis et distalis,” which is seemingly also a deep flexor muscle of the leg originally. The correspondence of this “transversus plantae proximalis et distalis” and the flexor accessorius medialis/lateralis of the hindlimb of urodeles seems clear, because the latter usually also originates at least partially from the fibulare and inserts onto the dorsal surface of the plantar fascia, running also in a fibulo-tibial direction. In fact, in derived anurans the muscle is often divided into proximal and distal bundles that resemble the flexor accessorius medialis and flexor accessorius lateralis of the urodele hindlimb, respectively. However, according to Dunlap (1960) in anurans the “transversus plantae proximalis et distalis” is plesiomorphically not divided into distal and proximal bundles so these bundles are not directly homologous to the two muscles of urodeles because they were seemingly not present in the last common ancestor of anurans; the undivided muscle of plesiomorphic anurans thus clearly seems to correspond to the usually also undivided flexor accessorius of the anuran forelimb. In summary, it would be difficult to accept that the so-called “tibialis posticus” of anurans really corresponds to the tibialis posterior sensu the present work, i.e. to the “pronator profundus” of urodeles, because that would mean that in anurans the “pronator profundus” is well separated, both ontogenetically and topologically, from all the other original deep flexors of the leg (i.e., the contrahentium caput longum, the flexor accessorius and the interosseus cruris). The structure that is often named “tibialis posticus” in anurans seems therefore to correspond to the flexor cruris et tarsi tibialis, which in urodeles corresponds very likely to the distal (leg) part of the ischioflexorius, as pointed out by authors such as McMurrich (1905) and Bardeen (1906).

popliteus of the mammalian leg seem to “correspond,” respectively, to the flexor carpi radialis and pronator teres of the mammalian forearm due to the absence of the HL muscle palmaris profundus 1 and the FL muscle pronator accessorius in mammals (Table 14). Interestingly, the configuration of these muscles in mammals is mirrored in phylogenetically derived reptilian groups such as crocodylians, in which the HL muscles popliteus and tibialis posterior are also remarkably similar topologically to the pronator teres and flexor carpi radialis, respectively (Table 20). These examples, which clearly illustrate the highly complex and homoplastic evolutionary history of the structures of the tetrapod FL and HL,

have been recognized previously by some researchers in their efforts to present evidence in support of the FL-HL serial homology hypothesis. For instance, Humphry (1872b) stated that the mammalian HL muscle tibialis posterior seems to “topologically correspond” to the mammalian FL muscle pronator teres but actually “corresponds ontogenetically” to the FL muscle palmaris profundus 1 of other tetrapods. He wrote that such examples “furnish a good illustration of the way in which certain nearly corresponding muscles in the two limbs are differently segmented from the parent mass; they afford further evidence that homological rule is not so rigidly followed in development as we may be

TABLE 8. Scheme illustrating hypotheses regarding the homologies of the foot muscles of adults of representative urodele and anuran amphibian taxa (see caption of Table 1)

	<i>Ambystoma mexicanum</i> [28 muscles]	<i>Xenopus laevis</i> [30 foot muscles]
	Flexores breves superficiales (5 muscles to d.1-5)	Flexores breves superficiales ('flexor digitorum brevis superficialis'; 3 muscles to d. 3-5; also gave rise to 'pl.pr.' and/or 'ta.po.')
	---	Lumbricales ('lumbricales breves' plus 'lumbricales longi' and 'lumbricalis longissimus IV'; 8 muscles to d.2-5) ^{2A}
	---	--- (but abductor prae hallucis present in other anurans, going to prehallux) ^{2A}
	---	Abductor brevis plantaris hallucis (1 muscle, 1 muscle to m.I) ^{2A}
Intrinsic foot muscles	Abductor digiti minimi (1 muscle to m.V)	Abductor digiti minimi ('abductor brevis dorsalis digiti V'; 1 muscle to m.V) ^{2B}
	Contrahentes pedis (5 muscles to d.1-5)	Contrahentes pedis ('contrahentes digitorum'; 3 muscles to d.1, 2 and to m.V) ^{2B}
	---	--- (but 'opponens hallucis' present in other anurans, going to m.I) ^{2B}
	Flexores digitorum minimi (4 muscles to d.2-5)	Flexores digitorum minimi ('flexores teretes digitorum'; 2 muscles to d.2-5)
	Interphalangeus digiti 3 (1 muscle to d.3)	Interphalangeus digiti 3 (1 muscle to d.3)
	Interphalangei digiti 4 (2 muscles to d.4)	Interphalangei digiti 4 (2 muscles to d.4)
	---	Interphalangeus digiti 5 (1 muscle to d.5)
	Flexores breves profundi (10 muscles to d.1-5) ^{2C}	Flexores breves profundi ('flexores ossi metatarsales'; 2 muscles to m.II and III)
	---	Abductor brevis plantaris digiti V (1 muscle to m.V) ^{2C}
	---	Abductor proprius digiti IV (1 muscle to m.IV) ^{2C}
Intermetatarsales (4 muscles metatarsals 1-5)	Intermetatarsales (transversi metatarsi; 4 muscles connecting metatarsals 1-5)	

As can be seen in the names highlighted in bold there are some cases in which, although the muscle that is designated with a certain name in anurans does not directly correspond to the muscle designated with a similar name in humans, both the anuran and human muscles derive from a similar anlage/ancestral muscle: the anuran “flexor digitorum brevis superficialis” and the human flexor digitorum brevis derived from the flexores breves superficiales (N.B., it is not clear if the lumbricales were present, or not, in the last common ancestor of tetrapods because they are usually present in anurans and amniotes but not in urodeles: if they present in the last common ancestor of tetrapods then the anuran lumbricales would correspond directly to the human lumbricales; the abductor digiti minimi of anurans clearly seems to directly correspond to the abductor digiti minimi of the human foot). d., digits; m., metatarsals; pl.pr., plantaris profundus; ta.po., tarsalis posticus.

^{2A}Regarding the “plantaris profundus,” see Table 7. Concerning the abductor prae hallucis and abductor brevis plantaris hallucis, these muscles seem to derive from the same anlage because they are deeply blended in various anurans (e.g., Dunlap, 1960), and according to Ribbing (1938) these muscles derive from the lumbricales, but if cannot be discarded that they also/instead receive a contribution from the flexores breves superficiales.

^{2B}All the contrahentes, i.e. to all five digits, are present in plesiomorphic anuran taxa such as *Leiopelma* (Dunlap, 1960). Concerning the “opponens hallucis,” which is present in most anurans but not in *Xenopus*, Dunlap (1960) suggested that it derived from the contrahentes, but the hypothesis of authors such as Perrin (1892) that it derived instead from the flexores breves profundi cannot be discarded particularly because there is no flexor brevis profundus going directly to metatarsal 1.

^{2C}This work follows Gaupp’s (1896) idea that the abductor proprius digiti IV derives from the “flexor ossis metatarsi IV” due to the topology of the two muscles and the fact that they are innervated by the same nerve. That is, as the abductor brevis plantaris digiti V, the abductor proprius digiti IV seems to derive from the flexores breves profundi sensu the present work, although it cannot be discarded that is also/instead receives a contribution from the intermetatarsales.

disposed to think, and that we must not be too severe in our attempts to institute homeological comparison” (Humphry, 1872b; p 175).

Additional examples of FL-HL homoplasy are seen in the human foot and hand (Table 15). The phylogenetically derived human hand muscle adductor pollicis accessorius (“volaris primus of Henle”: Bello-Hellegouarch, 2012) is mirrored by the likewise derived foot muscle “interosseus plantaris hallucis” sensu Cihak (1972). The transverse and oblique heads of the adductor pollicis and the oblique head of the adductor hallucis develop from the anlage of contrahens 1, but the transverse head of the adductor hallucis develops from a different, neomorphic anlage of the contrahens layer (e.g., Cihak, 1972).

Table 16 shows that many of the apparent “topological correspondences” seen in anatomically plesiomorphic tetrapods such as urodeles have been lost in anurans, in which the only dorsal forearm/leg muscles or muscle groups with apparent “topological equivalents” in the other limb are the extensor digitorum/extensor digitorum longus, the dorsometacarpales/dorsometatarsales and the extensores digitorum breves/extensores digitorum breves. One reason for the marked topological difference between the dorsal leg and forearm muscles is that, in anurans, the greatly elongated tarsal bones

tibiale and fibulare functionally partially replace the tibia and fibula of other tetrapods. Consequently, some leg muscles have migrated distally to the tarsal region (N.B., developmental evidence suggests that the transformation of the anuran tibiale and fibulare represents a distal shift in the zeugo-autopodial border, i.e., these bones have acquired a zeugopodial [leg] identity; e.g., Wagner and Chiu, 2003; Diogo and Ziermann, 2014). Despite these transformations, the dorsal side of the forearm and the leg have the same number of muscles/muscle groups (eight; Table 16). Moreover, although the apomorphic (uniquely derived) dorsal muscles of the anuran forearm and leg are not topologically similar, they derive evolutionarily from “topologically corresponding” muscles. The apomorphic HL muscle tibialis anticus brevis derives from the extensor tarsi tibialis (Table 16), and the apomorphic FL muscle brachioradialis derives from the extensor carpi radialis (Diogo and Abdala, 2010). The apomorphic HL muscle peroneus derives from the extensor cruris et tarsi fibularis (Table 16), and the apomorphic FL muscle anconeus derives from the extensor antebrachii et carpi ulnaris (Diogo and Abdala, 2010). In yet another example of FL-HL integration and evolutionary convergence/parallelism, both the anuran FL and HL have dorsometatarsales/metacarpales series and lack an abductor et extensor

TABLE 9. Scheme illustrating hypotheses regarding the homologies of the appendicular pelvic and thigh muscles of adults of representative reptilian taxa (see caption of Table 1)

	<i>Trachemys scripta</i> [14 pelvic and thigh muscles]	<i>Timon lepidus</i> [15 pelvic and thigh muscles]	<i>Aligator mississippiensis</i> [14 pelvic and thigh muscles]	<i>Gallus gallus</i> [17 pelvic and thigh muscles]	
Dorsal mass	Posterior	Iliofemoralis	Iliofemoralis	Iliofemoralis	Iliotrochantericus externus (gluteus med. et min.)
		---	---	---	Iliotrochantericus caudalis
		---	---	---	Iliotrochantericus cranialis
		---	---	---	Iliotrochantericus medius
		Iliotibialis	Iliotibialis	Iliotibialis (3 heads)	Iliotibialis (Iliotibialis lateralis) ^{4A}
	Anterior	Tenuissimus (Iliofibularis)	Tenuissimus (Iliofibularis)	Tenuissimus (Iliofibularis)	Tenuissimus (Iliofibularis; part of biceps)
		---	---	---	Iliotibialis cranialis (Sartorius) ^{4A}
		Femorotibialis (3 heads)	Femorotibialis (3 heads in some lizards)	Femorotibialis (2 heads)	Femorotibialis (3 heads)
		Sartorius (ambiens)	Sartorius (ambiens) ^{2E}	Sartorius (ambiens; 2 heads)	Sartorius (ambiens)
		Puboischiofemoralis internus (2 heads)	Puboischiofemoralis internus (3 heads)	Puboischiofemoralis internus (2 heads)	Puboischiofemoralis internus (iliacus ; 3 heads)
Ventral mass	Adductors	Adductor femoris (ischiofemoralis)	Adductor femoris	Adductor femoris (2 heads)	Adductor femoris (puboischiofemoralis, adductor ; 2 heads)
		Pubotibialis	Pubotibialis	---	---
		Gracilis (puboischiotibialis)	Gracilis (puboischiotibialis; 3 heads)	Gracilis (puboischiotibialis)	---
		Flexor tibialis internus (2 heads)	Flexor tibialis internus (2 heads)	Flexor tibialis internus (4 heads)	Flexor tibialis internus (ischioflexorius; semimembranosus , f.c.m.) ^{4B}
		---	---	---	Flexor cruris lateralis accessorius (accessorius) ^{4B}
	Ischiobiceps	Flexor tibialis externus (might include fl.cr.ta.ti)	Flexor tibialis externus (seems to include fl.cr.ta.ti)	Flexor tibialis externus (might include fl.cr.ta.ti)	Flexor tibialis externus (caudilioflexorius; semitendinosus , f.c.l.) ^{4B}
		Caudofemoralis (caudi-iliofemoralis)	Caudofemoralis longus	Caudofemoralis longus	Caudofemoralis (piriformis; 2 heads)
		---	Caudofemoralis brevis	Caudofemoralis brevis	---
		Puboischiofemoralis externus (2 major heads)	Puboischiofemoralis externus (2 major heads)	Puboischiofemoralis externus (3 major heads)	Puboischiofemoralis externus (obturator ; 2 heads)
		Ischiotrochantericus	Ischiotrochantericus	Ischiotrochantericus	Ischiotrochantericus (ischiofemoralis)

The muscle that is usually named “piriformis” in birds is not homologous to the muscle designated with the same name in humans, because the last common ancestor of reptiles and mammals did not have a distinct muscle piriformis. There are however, a few cases (highlighted in bold) in which although the muscle that is designated with a certain name in birds does not directly correspond to the muscle designated with the same name in humans, both the avian and human muscles derive from a similar anlage/ancestral muscle: the avian “gluteus medius” and “gluteus minimus” and the human gluteus medius and gluteus minimus derive from the iliofemoralis, the avian “obturator” and the human obturator externus derive from the puboischiofemoralis externus, the avian “iliacus” and the human iliacus derive from the puboischiofemoralis internus, the avian “adductor” and human adductor brevis and at least part of the adductor magnus derive from the adductor femoris, part of the avian “biceps” and of the human biceps seemingly derive from the tenuissimus, at least part of the avian “semimembranosus” and “semitendinosus” and of the human semimembranosus and human semitendinosus derive respectively from the flexor tibialis internus and externus. An., anterior; f.c.l., flexor cruris lateralis; f.c.m., flexor cruris medialis; fl.cr.ta.ti., flexor cruris tarsi tibialis; Ischiotroch., ischiotrochantericus; med. et min., medius et minimus.

^{4A}According to Jones (1979) during ontogeny the superficial/anterior dorsal mass or iliotibialis of birds expands anteriorly to form the iliotibialis cranialis (“sartorius”), the topology of which resembles the sartorius of mammals. However, the development of the iliotibialis cranialis suggests instead a homology with either the mammalian rectus femoris or part of the superficial gluteals, all being superficial dorsal mass derivatives. The extreme anterior position of the avian “sartorius” makes the homology with the rectus femoris most likely, both arising just superficial and anterior to the femoral nerve trunk and vasti/femorotibialis muscles. However one cannot completely rule out a partial homology of the avian “sartorius” and the mammalian sartorius, because Jones (1979) shows how the superficial dorsal mass occasionally contributes a slip of mesenchyme to the mouse sartorius as well.

^{4B}According to Jones (1979) the “ischioflexorius” and caudilioflexorius of birds seem to correspond respectively to the heads 1 and 2 of the flexor tibialis internus of lizards, and the avian “accessory muscle” (flexor cruris lateralis accessorius sensu the present work) is probably either a slip of the gastrocnemius that has migrated proximally or a distal slip of the caudo-femoralis. However, more recent and extensive comparative works between birds and other reptiles such as Dilkes (2000) and Fechner (2009) point out that the flexor tibialis externus of crocodylians corresponds mainly to the “flexor cruris lateralis” (“semitendinosus” or “caudilioflexorius”) of birds, while the flexor tibialis internus of crocodylians corresponds mainly to the “flexor cruris medialis” (“semimembranosus” or “ischioflexorius”) of birds.

digiti 1 (because the short extensor to digit 1 is a completely separate muscle in both of these limbs).

As in the dorsal forearm/leg, many apparent “topological correspondences” between the ventral forearm/leg muscles have been lost in anurans (Table 17), but contrary to the former case, the number of ventral forearm muscles/muscle groups in anurans (eight; Diogo and Abdala, 2010) is not equal to the number of ventral leg muscles/muscle groups (six; Table 17). However, there is a single flexor accessorius in both the FL and HL, constituting an example of homoplasy/integration that is seemingly plesiomorphic for frogs (Table 17; N.B., because of the dramatic transformations of the anuran HL, in frogs such as *Xenopus* the leg muscle flexor accessorius has migrated distally and lies in the foot region; therefore, it is topologically very different from the forearm muscle flexor accessorius and is not shown in Table 17). Examples of integration/homoplasy are also found in the foot/hand, including the presence in both autopodia of “breves” and “longus” layers of lumbricales, which were likely independently acquired during anuran evolution (Table 18).

Unsurprisingly considering their marked functional differences, in birds there are fewer apparent “topological equivalents” between the leg-foot and forearm-hand (Table 20). On the contrary, the very different functions of the FL and HL in humans are not associated with marked divergence in muscle anatomy (Fig. 2; Tables 13–15; see also above and Diogo et al., 2013). However, the FL and HL of birds provide an additional example of integration/homoplasy, despite their functional and anatomical divergence: in both limbs, the flexores breves superficiales have migrated proximally to the forearm and leg regions, respectively (e.g., Vanden Berge, 1975; Diogo and Abdala, 2010; this work).

DISCUSSION

Evolution of Tetrapod Hindlimb Muscles and Comparison with Forelimb Muscles

From the perspective of human evolution, salamanders, lizards, and rats are successively more closely

TABLE 10. Scheme illustrating hypotheses regarding the homologies of the dorsal/extensor leg muscles of adults of representative reptilian taxa (see caption of Table 1).

	<i>Trachemys scripta</i> [11 dorsal/extensor leg muscles]	<i>Timon lepidus</i> [9 dorsal/extensor leg muscles]	<i>Alligator mississippiensis</i> [8 dorsal/extensor leg muscles]	<i>Gallus gallus</i> [8 dorsal/extensor leg muscles]
Long extensors	Extensor digitorum longus (m.IV and d.1)	Ex. digitorum longus (m.II-III, not to digits)	Extensor digitorum longus (m.I-III, sometimes also to m.IV)	Ex. digitorum longus (to d. 2-4)
	Tibialis anterior	Tibialis anterior	Tibialis anterior	Tibialis anterior (tibialis cranialis)
	Fibularis longus (m.V and d.5)	Fibularis longus	Fibularis longus	Fibularis longus
	Fibularis brevis	Fibularis brevis	Fibularis brevis	Fibularis brevis
Short extensors	Extensores digitorum breves (3 muscles to d.2-4)	Extensores digitorum breves (4 muscles to d.2-5 + part short ex. d.1)	Extensores digitorum breves (3 muscles to d.2-4)	Extensores digitorum breves (3 muscles to d.2-4)
	Dorsometarsales (interossei dorsales; 3 muscles to d.2-4)	---	---	---
	Ab. et ex. digiti I (ex.h.p.+ab.h.; d.1; ab. + short ex. d.1) ^{1A}	Ab. et ex. digiti I (to d.1; ab. + part short ex. d.1)	Ab. et ex. digiti I (ex.h.l.; d.1; ab. + short ex. d.1)	Ab. et ex. digiti I (ex.h.l.; d.1; ab. + short ex. d.1)

The extensor digitorum longus, tibialis anterior, fibularis brevis, fibularis longus and extensores digitorum breves of birds clearly correspond to the muscles designated by similar names in humans. However, the “extensor hallucis longus” in birds is not homologous to the muscle designated with the same name in humans, because the last common ancestor of reptiles and mammals did not have a distinct extensor hallucis longus, and moreover the bird muscle corresponds to the abductor et extensor digiti 1 sensu the present work while the human extensor hallucis longus derives from the extensor digitorum longus. ab., abductor; ab.h., abductor hallucis; d., digits; ex., extensor; ex.h.l., extensor hallucis longus; ex.h.p., extensor hallucis proprius; m, metatarsals.

^{1A}In *Trachemys scripta* and various other turtles the “extensor hallucis proprius” runs from the distal fibula to the proximal phalanx of digit 1, thus corresponding to the abductor part of the abductor et extensor digiti 1 sensu the present work, while the “abductor hallucis” runs from the tarsal and metatarsal regions to the distal phalanx of digit 1, thus corresponding to the extensor part of the abductor et extensor digiti 1 sensu the present work, because these two structures are blended as recognized by Walker (1973).

related and morphologically more similar to modern humans (Fig. 2). Therefore, differences between the taxa in this study are interpreted in terms of the most parsimonious sequence of anatomical changes based on these phylogenetic relationships (e.g., when we say “the number of FL muscles increased from lizards to rats”). Salamanders are referred to as “anatomically plesiomorphic” relative to other taxa in this study because, morphologically, they closely resemble the hypothetical common ancestor of salamanders and other tetrapods, as extant lizards closely resemble the common ancestor of lizards, rats and humans (for a recent review on this subject, see Diogo et al., in press-a).

The total number of HL muscles in axolotls, the lizard *Timon*, rats, and modern humans is 55, 57, 57, and 61, respectively (Tables 1–4), while the total number of FL muscles is 49, 66, 65, and 59, respectively (Diogo et al., 2013, this work). This result demonstrates a case of mosaic evolution: salamanders and modern humans have more HL than FL muscles, while lizards and rats have more FL than HL muscles. Considering each region separately, there is a clear increase in the number of pelvic/thigh muscles from salamanders (N = 12) to lizards (N = 15) and to rats (N = 25), which have the same number as modern humans (N = 25) (Table 1). Interestingly, a similar trend is seen in the pectoral/arm muscles: salamanders have exactly the same number of pectoral/arm muscles and pelvic/thigh muscles (N = 12) and lizards and rats have almost the same number (N = 16 vs. 15 and N = 23 vs. 25, respectively). Modern humans are the exception; the pectoral/arm muscles were simplified in the evolutionary transitions that led to this clade (N = 18 vs. 25) (Diogo and Wood, 2012; Diogo et al., 2013, this work). However, the numbers given above for the pectoral/arm muscles include axial muscles, i.e. non-appendicular muscles connecting the axial skeleton to the pectoral girdle, while the pelvic/thigh muscles shown in Tables 1 to 12 are all appendicular muscles inserting directly onto the thigh or leg.

The number of ventral forearm muscles is constant across the four taxa (N = 8; Diogo et al., 2013; this work) and thus contrasts with the number of ventral leg muscles, which increases from salamanders and lizards

(N = 6) to rats (N = 7) and to modern humans (N = 8) (Table 3). There is a notable difference between the dorsal musculature of the forearm and leg: the number of dorsal leg muscles is essentially constant in salamanders, lizards and rats (N = 9) and modern humans (N = 10) (Table 2), while in the dorsal forearm there is a marked increase from salamanders (N = 8) to lizards (N = 14) and then a decrease to rats (N = 11) and a slight increase to modern humans (N = 12), the latter still having 1.5 times as many muscles as salamanders (Diogo et al., 2013; this work). There is a completely different pattern in the foot, with a consistent decrease from salamanders (N = 28) to lizards (N = 25) to rats (N = 22) and to modern humans (N = 21) (Table 4). The main reason for this decrease is the loss of entire groups of muscles, such as the flexores breves superficiales, contrahentes, intermetacarpales and intermetacarpales, during the evolutionary transitions leading to the mammalian clade in general and to modern humans in particular. A similar trend is seen in the hand: lizards have 29 muscles, rats have 25 and modern humans have 21, the difference being that salamanders such as axolotls have fewer hand muscles than lizards have (N = 23), mainly because salamanders have only four hand digits (Diogo and Tanaka, 2012, this work). However, the frog *Rana*, which also has four hand digits, has 29 muscles in the hand (Diogo and Abdala, 2010, this work).

Additional comparisons between salamanders and anurans support the idea that the evolution of the HL musculature mirrors that of the FL. For instance, axolotls have 23 hand and 28 foot muscles, while frogs have 29 hand and 30 foot muscles (*Rana* and *Xenopus*, respectively; this work, Table 8). Axolotls have 12 pectoral/arm muscles and 12 pelvic/thigh muscles, while frogs have 16 (*Rana*) and 17 (*Xenopus*), respectively (Diogo and Abdala, 2010; this work, Table 5). Axolotls have eight dorsal forearm muscles and nine dorsal/extensor leg muscles, while frogs have 15 (*Rana*) and 16 (*Xenopus*), respectively (Diogo and Abdala, 2010; this work, Table 6). Finally, both axolotls and *Rana* have the same number of ventral forearm muscles (N = 8; Diogo and Abdala, 2010, this work), and axolotls and *Xenopus* have the same number of ventral leg muscles (N = 6; Table 7).

TABLE 11. Scheme illustrating hypotheses regarding the homologies of the ventral/flexor leg muscles of adults of representative reptilian taxa (see caption of Table 1)

	<i>Trachemys scripta</i> [5 ventral/flexor leg muscles]	<i>Timon lepidus</i> [6 ventral/flexor leg muscles]	<i>Alligator mississippiensis</i> [7 ventral/flexor leg muscles]	<i>Gallus gallus</i> [4 ventral/flexor leg muscles]
	--- (fl.cr. ta.ti. seems included in fl.ti.ex. and/or ga.in.)	--- (fl.cr. ta.ti. seems included in fl.ti.ex. and eventually gain)	--- (fl.cr. ta.ti. seems included in fl.ti.ex. and/or ga.in.)	--- (fl.cr. ta.ti. seems included in ga.co. or lost)
Long flexors	---	---	Gastrocnemius plantaris (plantaris) ^{3A}	Gastrocnemius plantaris (plantaris) ^{4A}
	Gastrocnemius internus ('gastrocnemius'; 2 heads)	Gastrocnemius internus ('femorotibial')	Gastrocnemius internus	Gastrocnemius (3 heads)
	Gastrocnemius externus ('f.d.l. sublimis')	Gastrocnemius externus ('femoral'; sup. and deep heads)	Gastrocnemius externus	---
	Flexor digitorum communis (to d.1-4)	Flexor digitorum longus (to d.1-5)	Flexor digitorum longus (d.1-4)	Flexor digitorum longus (f.d.l.+f.h.l.; to d.1-4)
	--- (but some turtles have a popliteus) ^{1A}	Popliteus	Popliteus	Popliteus
	Interosseus cruris ^{1A}	Interosseus cruris	Interosseus cruris	---
	Tibialis posterior ('pronator profundus') ^{1A}	Tibialis posterior ('pronator profundus')	Tibialis posterior ('pronator profundus')	---

The flexor digitorum longus, popliteus and gastrocnemius of humans mainly correspond to at least part of the muscles designated by similar names in birds. However, the muscle that is usually named “plantaris” in birds is not homologous to the muscle designated with the same name in humans, because the last common ancestor of reptiles and mammals did not have a distinct plantaris muscle, thence we use a different name in birds. But, although the “plantaris” of birds does not directly correspond to the plantaris of humans, both the avian and human muscles derive from a similar anlage/ancestral muscle, i.e. from the gastrocnemius complex, thence the avian muscle is highlighted in bold. Regarding the avian “flexor hallucis longus,” although this structure and the extensor hallucis logus of humans are both derived from the flexor digitorum longus, the avian structure is simply a bundle of the flexor digitorum longus and not a separate muscle, in fact the last common ancestor of reptiles and mammals did not have a distinct flexor hallucis longus. d., digits; fl.cr.ta.ti., flexor cruris tarsi tibialis; f.d.l., flexor digitorum longus; f.h.l., flexor hallucis longus; fl.ti.ex., flexor tibialis externus; ga.co., gastrocnemius complex; ga.in., gastrocnemius internus; sup. superficial.

^{1A}Notes: The “popliteus” sensu Walker (1973) connects the tibia and fibula and is deep to the tibialis posterior, so it clearly corresponds to the interosseus cruris sensu the present work. According to Walker (1973) some turtles have however, “proximosuperficial” and “distodeep” portions, which are apparently similar, respectively, to the popliteus and interosseus cruris of other reptiles such as lizards, so this indicates that the popliteus does not derive from the flexor digitorum communis/gastrocnemius anlage, but instead from the interosseus cruris anlage (see Table 3).

^{3A,4A}The “plantaris” of birds and crocodylians is similar to the plantaris of mammals such as humans because it lies deep to and derives from the gastrocnemius complex, but it is almost surely the result of an evolutionary parallelism because the last common ancestor of amniotes and of reptiles seemingly did not have a muscle plantaris. The “plantaris” of birds is functionally and topologically different from that of mammals, e.g. not inserting onto the calcaneal region or with the flexor digitorum brevis and not originating from the femur as it typically does in various mammals but instead from the proximal tibia, i.e. it is a much shorter (proximodistally) muscle that is actually very short in most birds, as noted by Vanden Berge (1975), thence the use of the name plantaris gastrocnemius plantaris in the present work. However, it should be noted that the “plantaris” of crocodylians such as *Alligator* is actually a long muscle that runs from the distal end of the thigh muscles to both the calcaneal region and the flexor digitorum brevis, as usually does the plantaris of mammals, so it is possible that the last common ancestor of birds and crocodylians did have a condition that is quite similar to that of the plantaris of mammals.

Within reptiles, the number of pectoral and arm muscles increases from the turtle *Trachemys* (N = 14) to the lizard *Timon* (N = 16) and again to the crocodylian *Alligator* and the bird *Gallus* (N = 17) (N.B., lizards, crocodylians, and birds are more closely related to each other than any of these groups is to turtles). A similar trend is seen in the pelvic and thigh musculature, with an increase from turtles (N = 14) to lizards (N = 15) and again to birds (N = 17); crocodylians are the exception with only 14 pelvic/thigh muscles (Table 9). There is an opposing trend in the number of dorsal leg muscles, with a decrease from turtles (N = 17) to lizards (N = 9) to crocodylians and birds (N = 8) (Table 10). The number of dorsal forearm muscles also decreases from turtles (N = 17) to lizards (14) to birds (10), crocodylians again being the exception with 17 dorsal forearm muscles (Diogo and Abdala, 2010; this work). Similar trends were observed in the hand and foot, i.e., an increase from turtles (N = 17 hand and 20 foot muscles) to lizards (N = 29 and 25, respectively) and a decrease to crocodylians (N = 25, 21) and to birds (N = 7, 10) (Diogo and Abdala, 2010; Table 12, this work). The number of ventral forearm muscles decreases from turtles (N = 9) to lizards (N = 8) to crocodylians (N = 6) and increases in birds (N = 7) (Diogo and Abdala, 2010; this work), whereas the number of ventral leg muscles increases from turtles (N = 5) to lizards (N = 6) to crocodylians (7) and

decreases in birds (N = 4) (Table 11). In summary, with exception of the ventral forearm and leg muscles, there is an evolutionary pattern of integration/homoplasy in the number of FL and HL muscles within reptiles. However, crocodylians do not follow the general reptilian pattern in pectoral-arm/pelvic-thigh or dorsal forearm/leg musculature.

The results of the present study and the use of a unifying nomenclature for HL muscles across the whole tetrapod clade (Tables 1–12) have the potential to solve some major comparative problems in tetrapod evolution and anatomy. For instance, classical authors such as Ecker (1864) compared human muscles with those of frogs and birds without taking into account the configuration found in anatomically more plesiomorphic reptiles and amphibians, thus erroneously using the same names for non-homologous muscles. Unfortunately, many of these names are still used in current textbooks, ontologies and specialized articles. An illustrative example is Prikryl et al.’s (2009) study, which is otherwise excellent but uses names of human muscles to designate several non-homologous pelvic-thigh muscles of frogs. Only one pelvic-thigh muscle that was present in the most recent common ancestor of amphibians and amniotes actually seems to be homologous with an individual human pelvic-thigh muscle (the gracilis; Tables 1 and 5). This confusing nomenclature is a major problem not only for comparative anatomy in general, but also for amphibian

TABLE 12. Scheme illustrating hypotheses regarding the homologies of the foot muscles of adults of representative reptilian taxa (see caption of Table 1)

	<i>Trachemys scripta</i> [20 muscles]	<i>Timon lepidus</i> [25 foot muscles]	<i>Aligator mississippiensis</i> [at least 21 foot muscles]	<i>Gallus gallus</i> [10 foot muscles]
Intrinsic foot muscles	Flexores breves sup. (fl.di.com.sub.; 4 muscles to d.1-4)	Flexores breves sup. (3 muscles to d.1-3)	Flexores breves sup. (4 muscles to d.1-4)	Flexores breves sup. (f.p.II,III + f.p.II,III,IV; 5 muscles to d.2-4)
	Lumbricales (4 muscles to d.2-5)	Lumbricales (2 muscles to d.3-4)	Lumbricales (4 muscles, to d.1-4)	Lumbricales (2 muscles, to d.3-4)
	—	Abductor digiti minimi (1 muscle to m.V)	Abductor digiti minimi (mainly to m.IV)	Abductor digiti minimi ('ab.di.IV'; 1 muscle to d.4)
	Contrahentes pedis (p.i.p.; 4 muscles to d.1-4) ^{1A}	Contrahentes pedis (5 muscles to d.1-5)	Contrahentes pedis (at least 1 muscle to d.1)	Contrahentes pedis ('adductor digiti II'; 1 muscles to d.2)
	Flexores breves profundi (p.i.p.; 4 muscles to d.1-4) ^{1A}	Flexores breves profundi (10 muscles to d.1-5)	Flexores breves profundi (seemingly 8 muscles to d.1-4)	Flexores breves profundi (Fl.h.b. ; 1 muscle to d.1)
Intermetatarsales (p.i.p.; 4 muscles connecting m.1-5) ^{1A}	Intermetatarsales (4 muscles connecting m.1-5)	Intermetatarsales (seemingly 3 muscles connecting m.1-4)	—	

The flexores breves superficiales, lumbricales and abductor digiti minimi of birds clearly correspond to the muscles designated by similar names in humans. Regarding the avian “flexor hallucis brevis,” this muscle corresponds to the first flexor brevis profundi, so it does correspond to the flexor hallucis brevis of humans sensu the present work (i.e. to the structure usually designated as “medial head of the flexor hallucis longus” in human anatomy). However, in the last common ancestor of tetrapods and of amniotes this first flexor brevis profundi was clearly part of a group of muscles, the flexores breves profundi, and was not a distinct, separate, peculiar muscle as is the case in birds and humans, so the bird and human condition is the result of an evolutionary homoplasy (thence the bird muscle is highlighted in bold). ab.di.IV, abductor digiti IV; d., digits; fl.di.com.sub., flexor digitorum communis sublimis; f.h.b., flexor hallucis brevis; f.p.II,III + f.p. II,III,IV; flexor perforans et perforatus digiti II and III plus flexor perforatus digiti II, III and IV; m, metatarsals; p.”i.p.” part of “interossei plantares” sensu Walker 1973; sup., superficiales.

^{1A}Walker (1973) states that in turtles such as *Trachemys scripta* the “interossei plantares” run from tarsals and metatarsals to the fibular side of the proximal phalanges of digits 1–4. His descriptions and particularly his illustrations (see, e.g., his figs. 25 and 30) as well as the fact that he recognized that his “interossei plantares” correspond to the flexores breves profundi, contrahentes and “interdigitales” sensu Ribbing (1938) clearly indicate that his “interossei plantares” do include the flexores breves profundi (thus probably 4 muscles to digits 1–4), contrahentes (thus probably 4 muscles to digits 1–4) and intermetatarsales (thus probably 4 muscles connecting the metatarsals 1–5, i.e. inserting onto metatarsals 1–4) sensu the present work.

comparative anatomy and broader evolutionary biology because different names are used to designate homologous muscles in frogs and salamanders (see, e.g., Table 2 of Prikryl et al., 2009). In fact, as recognized by Prikryl et al. (2009), many researchers still follow anuran and urodelan muscle nomenclatures published several decades ago (see, e.g., Gaupp, 1896 for anurans and Francis, 1934 for urodeles), when many authors did not consider frogs and salamanders to be closely related to each other (see, e.g., Edgeworth, 1935).

Deconstruction of the Forelimb-Hindlimb Serial Homology Hypothesis

The previous section provides several examples of HL muscles that mirror the evolution of the FL muscles in each major tetrapod clade and in Tetrapoda as a whole. Combined with the data provided in the Results section, these examples strongly support the idea that a substantial number of FL-HL similarities found in extant tetrapods result from parallelism/convergence (homoplasy) during the evolutionary history of these clades, and not from serial homology (i.e., ancestral duplication of the structures of the paired appendages). As explained in the Introduction, Diogo et al. (2013) provided an extensive review of several lines of evidence—published by other researchers—that contradict arguments often used to support the FL-HL serial homology hypothesis. Curiously, the researchers themselves did not question or contradict the serial homology hypothesis, which continues to be treated as dogma by many.

The failure to question and contradict this hypothesis and ultimately to recognize that FL-HL serial homology is an unfounded assumption is mainly due to four factors. The first is the recurrent citation of older authors such as Vicq d’Azyr (1774), Oken (1843), and Owen (1849) without a detailed, critical analysis of their original works (see Introduction). The second is the almost

exclusive focus on bones in anatomical studies. The third, which is related to the former two and to the decline of evolutionary vertebrate morphology, is the scarcity of detailed, unbiased comparisons of both the hard and soft tissues across the major vertebrate clades. The final reason is the lack of integration of new data from comparative anatomy, developmental biology, genetics, paleontology, functional morphology and evolutionary biology with older, classical texts.

The final refutation of the “paired appendages serial homology followed by functional/anatomical divergence” hypothesis (Fig. 1) comes from such an integrative analysis combined with the first detailed examination and comparison of the soft tissues of the paired appendages in representatives of all major extant gnathostome clades (Fig. 2). As noted in Fig. 2, the PEC and PEL of extant plesiomorphic gnathostome fish have largely undifferentiated adductor and abductor muscle masses (e.g., Diogo and Abdala, 2010). Therefore, all of the numerous and (as will be seen below) in many cases strikingly similar muscles, as well as the various bones (e.g., Don et al., 2012), of the tetrapod FL and HL were undoubtedly acquired independently during the evolutionary transitions between early gnathostomes and tetrapods. Therefore, under the historical (phylogenetic) definition of homology, these structures cannot be considered serial homologues. One could argue that they are homologous under the morphological or developmental definitions (see Wagner, 1994), but this argument is contradicted by analysis of the evolution of the soft tissues of the gnathostome paired appendages, particularly the muscles (see Results; Tables 1–21).

As explained in the Introduction, ancestral morphological or developmental serial homology of the FL and HL implies that they were originally similar and then diverged anatomically/functionally (Fig. 1). On the contrary, the hard tissues of the PEC and PEL plesiomorphically were anatomically very different (Zhu et al., 2012)

TABLE 13. Scheme illustrating the “clear topological correspondences” between the dorsal leg and forearm muscles of adults of representative tetrapod taxa

	<i>Ambystoma mexicanum</i> [6 dorsal/extensor leg muscles/muscle groups: 6 (100%) seem to 'correspond' directly to forelimb muscles/muscle groups]	<i>Timon lepidus</i> [6 dorsal/extensor leg muscles/muscle groups: 4 (67%) seem to 'correspond' directly to forelimb muscles/muscle groups]	<i>Rattus norvegicus</i> [8 dorsal/extensor leg muscles/muscle groups: 3 (38%) seem to 'correspond' directly to forelimb muscles/muscle groups]	<i>Homo sapiens</i> [8 dorsal/extensor leg muscles/muscle groups: 3 (38%) seem to 'correspond' directly to forelimb muscles/muscle groups]
Long extensors	---	---	Extensor hallucis longus (d. 1) <i>[Extensor pollicis longus]</i>	Extensor hallucis longus (d. 1) <i>[Extensor pollicis longus]</i>
	Extensor digitorum longus ('extensor digitorum communis'; m.I-V) <i>[Extensor digitorum]</i>	Extensor digitorum longus (m.II-III, not to digits) <i>[Extensor digitorum]</i>	Extensor digitorum longus (d. 2-5) <i>[Extensor digitorum]</i>	Extensor digitorum longus (d. 2-5) <i>[Extensor digitorum]</i>
	Extensor tarsi tibialis <i>[Extensor carpi radialis]</i>	Tibialis anterior <i>[Extensor antebrachii et carpi radialis]</i>	Tibialis anterior	Fibularis tertius (m.V) Tibialis anterior
	Extensor cruris tibialis <i>[Supinator]</i>	---	---	---
Short extensors	Extensor cruris et tarsi fibularis <i>[Extensor antebrachii et carpi ulnaris]</i>	Fibularis longus	Fibularis longus	Fibularis longus
	---	Fibularis brevis	Fibularis brevis	Fibularis brevis
	Extensores digitorum breves (4 muscles to d.2-5) <i>[Extensores digitorum breves]</i>	Extensores digitorum breves (4 muscles to d.2-5 + part short ex. d.1) <i>[Extensores digitorum breves]</i>	Fibularis digiti quarti (m.IV in rats and d.4 in mice) Fibularis digiti quinti (m.V in rats and d.5 in mice) Extensor digitorum brevis (2 muscles to d.2-3) <i>[Extensor indicis]</i>	Extensor digitorum brevis (3 muscles to d.2-4) <i>[Extensor indicis]</i>
	Abductor et ex. digiti I (d.1; abductor + part short ex. d.1) <i>[Abductor et ex. digiti I]</i>	Abductor et ex. digiti I (d.1; abductor + part short ex. d.1) <i>[Abductor pollicis longus]</i>	---	Extensor hallucis brevis (d.1; short ex. d.1) <i>[Extensor pollicis brevis]</i>

Below the names of those hindlimb muscles/muscle groups that have clear, direct topological forelimb “equivalents” in the same taxon, the names of those forelimb “equivalents” are provide (in red, between square brackets). In those cases in which those “equivalents” clearly have a different ontogeny, these are shown in italics. d., digits; ex., extensor; ex.ha.br., extensor hallucis brevis; m, metatarsals (attachments are in general only shown for muscles that often insert onto digits).

TABLE 14. Scheme illustrating the “clear topological correspondences” between the ventral leg and forearm muscles of adults of representative tetrapod taxa (see caption of Table 13)

	<i>Ambystoma mexicanum</i> [6 ventral/flexor leg muscles/muscle groups: 6 (100%) seem to 'correspond' directly to forelimb muscles/muscle groups]	<i>Timon lepidus</i> [6 ventral/flexor leg muscles/muscle groups: 4 (67%) seem to 'correspond' directly to forelimb muscles/muscle groups]	<i>Rattus norvegicus</i> [7 ventral/flexor leg muscles/muscle groups: 4 (57%) seem to 'correspond' directly to forelimb muscles/muscle groups]	<i>Homo sapiens</i> [8 ventral/flexor leg muscles/muscle groups: 5 (62%) seem to 'correspond' directly to forelimb muscles/muscle groups]
Long flexors	--- (fl.cr.ta.ti. seems included in ischioflexorius)	--- (fl.cr.ta.ti. seems included in fl.ti.ex. and eventually ga.in.)	--- (fl.cr.ta.ti. seems included in ha.fa. and eventually ga.)	--- (fl.cr.ta.ti. seems included in ha.fa. and eventually ga.)
	---	Gastrocnemius internus ('femorotibial')	Gastrocnemius (medial and lateral heads)	Gastrocnemius (medial and lateral heads)
	---	Gastrocnemius externus ('femoral'; sup. and deep heads)	Plantaris <i>[Palmaris longus]</i>	Plantaris <i>[Palmaris longus]</i>
	---	---	Soleus	Soleus
	Fl. dig. com. (d.1-5; includes fl.cr.ta.fi.) <i>[Flexor digitorum communis]</i>	Flexor digitorum longus (d. 1-5) <i>[Flexor digitorum longus]</i>	Flexor digitorum longus (d. 1-5) <i>[Flexor digitorum profundus]</i>	Flexor digitorum longus (d. 2-5) <i>[Flexor digitorum profundus]</i>
	---	---	---	Flexor hallucis longus (d. 1) <i>[Flexor pollicis longus]</i>
	Flexor accessorius medialis <i>[Flexor accessorius medialis]</i>	--- ('flexor accessorius' is distal head of flexor digitorum longus)	Quadratus plantae	Quadratus plantae
	Flexor accessorius lateralis <i>[Flexor accessorius lateralis]</i>	---	---	---
	Contrahentium caput longum <i>[Contrahentium caput longum]</i>	---	---	---
	---	Popliteus <i>[Pronator accessorius]</i>	Popliteus <i>[Pronator teres]</i>	Popliteus <i>[Pronator teres]</i>
Interosseus cruris <i>[Pronator quadratus]</i>	Interosseus cruris <i>[Pronator quadratus]</i>	---	---	
Tibialis posterior ('pronator profundus') <i>[Palmaris profundus 1]</i>	Tibialis posterior ('pronator profundus') <i>[Palmaris profundus 1]</i>	Tibialis posterior <i>[Flexor carpi radialis]</i>	Tibialis posterior <i>[Flexor carpi radialis]</i>	

d., digits; fl.cr.ta.fi., flexor cruris tarsi fibularis; fl.cr.ta.ti., flexor cruris tarsi tibialis; fl.dig.com., flexor digitorum communis; fl. ti.ex., flexor tibialis externus; ga., gastrocnemius; ga.in., gastrocnemius internus; ha.fa., fascial insertion of hamstring muscles; sup. superficial.

and both the hard and soft tissues of the proximal region of the PEC and PEL (particularly the girdles) have remained markedly different in all gnathostome clades (Coates and Cohn, 1998; Diogo et al., 2013; Fig. 2; Tables 1–21, this work). For instance, within all tetrapod clades listed in Fig. 2 and Tables 13 to 21, including anatomically plesiomorphic taxa such as urodeles (Fig. 3), not even one pelvic-thigh muscle has a clear “topological equivalent” in the pectoral region and arm. This lack of equivalence seems to be due to a strong phylogenetic constraint; i.e., the pelvic and pectoral girdles of fish plesiomorphically were markedly different anatomically, and consequently the girdles of tetrapods are also quite different. However, the derived distal regions of the tetrapod FL and HL, particularly the autopodium (hand/foot), have at least some new bones and a very different developmental plan from the PEC and PEL in fish [N.B., even if digits are derived from distal fin rays as

suggested by, e.g., Johanson et al. (2007); see also, e.g., Davis et al. (2007), it is broadly accepted that at least some tetrapod wrist/ankle bones are neomorphic structures; e.g., Don et al. (2012)]. Therefore, the evolution of the autopodium represents a major “evolutionary novelty” and is subject to fewer phylogenetic constraints than the limb girdles, and the developmental constraints/factors resulting from further derived (e.g. Roth 1994) co-option of some similar genes in the ontogeny of the FL and HL led to greater similarity between the distal regions of these limbs in basal tetrapods (“similarity bottleneck”: Fig. 2).

The detailed data on the tetrapod hindlimb muscles obtained in the present study supports this hypothesis and complements the information about the forearm-hand and leg-foot muscle similarities provided by Diogo et al. (2013). The percentage of ventral leg muscles with “topological equivalents” in the FL decreases from salamanders (100%)

TABLE 15. Scheme illustrating the “clear topological correspondences” between the hand and foot muscles of adults of representative tetrapod taxa (see caption of Table 15)

	<i>Ambystoma mexicanum</i> [7 foot muscles/muscle groups: 7 (100%) seem to 'correspond' directly to forelimb muscles/muscle groups]	<i>Timon lepidus</i> [6 foot muscles/muscle groups: 6 (100%) seem to 'correspond' directly to forelimb muscles/muscle groups]	<i>Rattus norvegicus</i> [9 foot muscles/muscle groups: 9 (100%) seem to 'correspond' directly to forelimb muscles/muscle groups]	<i>Homo sapiens</i> [11 foot muscles/muscle groups: 11 (100%) seem to 'correspond' directly to forelimb muscles/muscle groups]
Intrinsic foot muscles	Flexores breves superficiales (5 muscles to d.1-5) [Flexores breves superficiales]	Flexores breves superficiales (3 muscles to d.1-3) [Flexores breves superficiales]	Flexor digitorum brevis (d.2-4) [Flexor digitorum superficialis]	Flexor digitorum brevis (d.2-5) [Flexor digitorum superficialis]
	---	Lumbricales (2 muscles, to d.3-4) [Lumbricales]	Lumbricales (4 muscles, to d.2-4) [Lumbricales]	Lumbricales (4 muscles to d.2-4) [Lumbricales]
	Abductor digiti minimi (m.V) [Abductor digiti minimi]	Abductor digiti minimi (m.V) [Abductor digiti minimi]	Abductor digiti minimi (d.5) [Abductor digiti minimi] --- (abductor hallucis seemingly fused with flexor hallucis brevis)	Abductor digiti minimi (d.5) [Abductor digiti minimi] Abductor hallucis (d.1) [Abductor pollicis brevis] * Interossei plantaris hallucis (d.1) [Adductor pollicis accessorius, or 'volaris primus of Henle']
	---	---	---	---
	Contrahentes pedis (5 muscles to d.1-5) [Contrahentes digitorum]	Contrahentes pedis (5 muscles to d.1-5) [Contrahentes digitorum]	Contrahentes pedis (2 muscles, to d.2,5) [Contrahentes digitorum]	---
	---	---	---	Adductor hallucis (oblique and transverse heads) [Adductor pollicis]
	---	---	Flexor digiti minimi brevis (= f.b.p. 10, to d.5) [Flexor digiti minimi]	Flexor digiti minimi brevis (= f.b.p. 10, to d.5) [Flexor digiti minimi]
	---	---	Flexor brevis profundus 2 (to fibular side of d.1) [Flexor brevis profundus 2]	Flexor brevis profundus 2 (fibular side of d.1) [Flexor brevis profundus 2]
	Flexores digitorum minimi (4 muscles to d.2-5) [Flexores digitorum minimi]	---	Flexor hallucis brevis (= f.b.p. 1, to tibial side of d.1) [Flexor pollicis brevis]	Flexor hallucis brevis (= f.b.p. 1, tibial side of d.1) [Flexor pollicis brevis]
	Interphalangei digiti 4 (2 muscles to d.4) [Interphalangei]	---	---	---
	Flexores breves profundi (10 muscles to d.1-5) [Flexores breves profundi]	Flexores breves profundi (10 muscles to d.1-5) [Flexores breves profundi]	Flexores breves profundi (3,4,5,6,7,8,9, i.e. 7 muscles to d.2,5) [Flexores breves profundi]	Interossei plantares (3 f.b.p. muscles to d.3,4,5) [Interossei palmares] Interossei dorsales (4 f.b.p. muscles + 4 interm. = 4 muscles, to d.2-4) [Interossei dorsales]
	Intermetatarsales (4 muscles connecting m.1-5) [Intermetacarpales]	Intermetatarsales (4 muscles connecting m.1-5) [Intermetacarpales]	Intermetatarsales (4 muscles connecting d.1-5) [Intermetacarpales]	---

d., digits; di., digitorum; f.b.p., flexores breves profundi; interm., intermetatarsales; m, metatarsals.

TABLE 16. Scheme illustrating the “clear topological correspondences” between the dorsal leg and forearm muscles of adults of representative urodele and anuran taxa (see caption of Table 13).

	<i>Ambystoma mexicanum</i> [6 dorsal/extensor leg muscles/muscle groups: 6 (100%) seem to 'correspond' directly to forelimb muscles/muscle groups]	<i>Xenopus laevis</i> [9 dorsal/extensor leg muscles/muscle groups: 3 (33%) seem to 'correspond' directly to forelimb muscles/muscle groups]
Long extensors	Extensor digitorum longus (extensor digitorum communis; m.I-V) [Extensor digitorum]	Extensor digitorum longus (to short extensors of digits 3 and 4) [Extensor digitorum]
	---	Tarsalis anticus Tibialis anticus brevis
	Extensor tarsi tibialis [Extensor carpi radialis]	---
	Extensor cruris tibialis [Supinator]	Extensor cruris tibialis ('extensor cruris brevis')
	Extensor cruris et tarsi fibularis [Extensor antebrachii et carpi ulnaris]	Peroneus
Short extensors	---	Tibialis anticus longus
	Extensores digitorum breves (4 muscles to d.2-5) [Extensores digitorum breves]	Dorsometatarsales [Dorsometacarpales] Extensores digitorum breves ('e.b.s.+e.b.m.+e.b.p.'; 5 muscles to d.1-5) [Extensores digitorum breves]
	Abductor et extensor digiti 1 (d.1; abductor + part short extensor d.1) [Abductor et extensor digiti 1]	Abductor brevis dorsalis hallucis (m.I)

As can be seen in the names highlighted in bold there are some cases in which, although the muscle that is designated with a certain name in anurans does not directly correspond to the muscle designated with a similar name in humans (but not the same, thence we can use the commonly used anuran names), both the anuran and human muscles derive from a similar anlage/ancestral muscle: the anuran “tibialis anticus brevis” and the human tibialis anterior (anticus) derive from the extensor tarsi tibialis, and the anuran “peroneus” and the human fibularis (peroneus) longus/brevis derive from the extensor cruris et tarsi fibularis (N.B., regarding the extensor digitorum longus and the extensores digitorum breves of anurans, they mainly correspond directly to the extensor digitorum longus and extensor digitorum brevis of humans, because they were present in the last common ancestor of tetrapods). As can also be seen, the presence of a single leg bone (cruris) and the remarkable proximodistal elongation of the tibiale and fibulare bones in anurans seems to have led to a functional convergence between these bones and the tibia and fibula of tetrapods such as urodeles, and consequently there are almost no “clear topological correspondences” between the muscles of the leg and forearm of anurans. d., digits; ext., extensors; “e.b.s.+ e.b.m.+e.b.p.,” “extensores breves superficiales” plus “extensores breves medii” sensu Dunlap 1960; m., metatarsals.

to lizards (67%) and to rats (57%) and then increases in humans (62%) (Table 14). Among the dorsal leg muscles, the percentage decreases from salamanders (100%) to lizards (67%) and again to rats (38%), which is equal to that in humans (38%) (Table 13). In all four taxa, 100% of foot muscles have a “topological equivalent” in the hand

(Table 15). The total percentage across all limb muscles decreases from salamanders (19 similarities within 19 muscles/muscle groups = 100%) to lizards (14/18 = 78%) and to rats (16/24 = 67%) and then increases in humans (19/27 = 70%). In a clear example of functional/anatomical divergence in the evolutionary

TABLE 17. Scheme illustrating the “clear topological correspondences” between the ventral leg and forearm muscles of adults of representative urodele and anuran taxa (see caption of Table 13)

	<i>Ambystoma mexicanum</i> [6 ventral/flexor leg muscles/muscle groups: 6 (100%) seem to 'correspond' directly to forelimb muscles/muscle groups]	<i>Xenopus laevis</i> [6 ventral/flexor leg muscles/muscle groups: 1 (17%) seem to 'correspond' directly to forelimb muscles/muscle groups]
Long flexors	Flexor digitorum communis (d.1-5; includes fl.cr.ta.fi.) [Flexor digitorum communis]	Flexor digitorum communis ('plantaris longus'; directly only to d.1-2) [Flexor digitorum communis]
	--- (fl.cr. ta.ti. seems to be included in ischioflexorius)	Cruroastragalus ('tibialis posticus'; seems to correspond to fl.cr.ta.ti.)
	Flexor accessorius medialis [Flexor accessorius medialis]	Flexor accessorius ('transversus plantae proximalis et distalis')
	Flexor accessorius lateralis [Flexor accessorius lateralis]	---
	Contrahentium caput longum [Contrahentium caput longum]	Contrahentium caput longum ('tarsalis posticus'; derived also/instead from fb.s?)
	Interosseus cruris [Pronator quadratus]	Interosseus cruris ('intertarsalis')
	Tibialis posterior ('pronator profundus') [Palmaris profundus 1]	Tibialis posterior ('plantaris profundus'; or 'palmaris profundus' derived instead from fb.s?)

As can be seen in the names highlighted in bold there are some cases in which, although the muscle that is designated with a certain name in anurans does not directly correspond to the muscle designated with a similar name in humans, both the anuran and human muscles derive from a similar anlage/ancestral muscle: the anuran plantaris longus and the human plantaris derive from the flexor digitorum communis (N.B., the anuran “tibialis posticus” and the human tibialis posterior do not seem to be homologous, as shown in this table). As can also be seen, the presence of a single leg bone (cruis) and the remarkable proximodistal elongation of the tibiale and fibulare bones in anurans seems to have led to a functional convergence between these bones and the tibia and fibula of tetrapods such as urodeles, and consequently there are almost no “clear topological correspondences” between the muscles of the leg and forearm of anurans. d., digits; f.b.s., flexores breves superficiales; fl.cr.ta.fi., flexor cruris et tarsi fibularis; fl.cr.ta.ti., flexor cruris et tarsi tibialis.

TABLE 18. Scheme illustrating the “clear topological correspondences” between the foot and hand muscles of adults of representative urodele and anuran taxa (see caption of Table 13)

	<i>Ambystoma mexicanum</i> [7 foot muscles/muscle groups: 7 (100%) seem to 'correspond' directly to forelimb muscles/muscle groups]	<i>Xenopus laevis</i> [11 foot muscles/muscle groups: 8 (73%) seem to 'correspond' directly to forelimb muscles/muscle groups]
Intrinsic foot muscles	Flexores breves superficiales (5 muscles to d.1-5) [Flexores breves superficiales]	Flexores breves superficiales ('flexor digitorum brevis superficialis'; 3 muscles to d. 3-5; also gave rise to 'pl.pr.' and/or 'ta.po.?) [Flexores breves superficiales]
	---	Lumbricales ('lumbricales breves' plus 'lumbricales longi' and 'lumbricalis longissimus IV'; 8 muscles to d.2-5) [Lumbricales]
	---	(but abductor praeahallucis present in other anurans, going to preahallux)
	---	Abductor brevis plantaris hallucis (1 muscle, 1 muscle to m.I)
	Abductor digiti minimi (1 muscle to m.V) [Abductor digiti minimi]	Abductor digiti minimi ('abductor brevis dorsalis digiti V'; 1 muscle to m.V) [Abductor digiti minimi]
	Contrahentes pedis (5 muscles to d.1-5) [Contrahentes digitorum]	Contrahentes pedis ('contrahentes digitorum'; 3 muscles to d.1, 2 and to m.V) [Contrahentes digitorum]
	---	(but 'opponens hallucis' present in other anurans, going to m.I)
	Flexores digitorum minimi (4 muscles to d.2-5) [Flexores digitorum minimi]	Flexores digitorum minimi ('flexores teretes digitorum'; 2 muscles to d.2-5) [Flexores digitorum minimi]
	Interphalangei (3 muscles to d.3-4) [Interphalangei]	Interphalangei (4 muscle to d.3-5) [Interphalangei]
	Flexores breves profundi (10 muscles to d.1-5) [Flexores breves profundi]	Flexores breves profundi ('flexores ossi metatarsales'; 2 muscles to m.II and III) [Flexores breves profundi]
---	Abductor brevis plantaris digiti V (1 muscle to m.V)	
---	Abductor proprius digiti IV (1 muscle to m.IV)	
Intermetatarsales (4 muscles metatarsals 1-5) [Intermetacarpales]	Intermetatarsales ('transversi metatarsi'; 4 muscles connecting metatarsals 1-5) [Intermetacarpales]	

As can be seen in the names highlighted in bold there are some cases in which, although the muscle that is designated with a certain name in anurans does not directly correspond to the muscle designated with a similar name in humans, both the anuran and human muscles derive from a similar anlage/ancestral muscle: the anuran “flexor digitorum brevis superficialis” and the human flexor digitorum brevis derived from the flexores breves superficiales (N.B., it is not clear if the lumbricales were present, or not, in the last common ancestor of tetrapods because they are usually present in anurans and amniotes but not in urodeles: if they present in the last common ancestor of tetrapods then the anuran lumbricales would correspond directly to the human lumbricales; the abductor digiti minimi of anurans clearly seems to directly correspond to the abductor digiti minimi of the human foot). d., digits; m, metatarsals; pl.pr., plantaris profundus; ta.po., tarsalis posticus.

history of amphibians, the total percentage of FL and HL limb muscles in the frog *Xenopus* with “topological equivalents” is 48% (12/25) (Tables 16–18), compared with 100% in anatomically more plesiomorphic amphibians such as axolotls (19/19). As explained in the Results section, this divergence is mainly related to the greatly elongated tibiale and fibulare in anu-

rans that functionally partially replaces the tibia and fibula. Even so, there are some remarkable examples of FL-HL muscle integration/homoplasy in anurans. Among reptiles, the total percentage in the lizard *Timon* is 78% (14/18) as noted above, and 77% (13/17), 74% (14/19), and 60% (9/15) (Tables 19–21) in turtles, alligators and birds, respectively.

TABLE 19. Scheme illustrating the “clear topological correspondences” between the dorsal/extensor leg and forerarm muscles of adults of representative reptilian taxa (see caption of Table 13)

	<i>Trachemys scripta</i> [7 dorsal/extensor leg muscles/muscle groups: 5 (71%) seem to 'correspond' directly to forelimb muscles/muscle groups]	<i>Timon lepidus</i> [6 dorsal/extensor leg muscles/muscle groups: 4 (67%) seem to 'correspond' directly to forelimb muscles/muscle groups]	<i>Alligator mississippiensis</i> [6 dorsal/extensor leg muscles/muscle groups: 4 (67%) seem to 'correspond' directly to forelimb muscles/muscle groups]	<i>Gallus gallus</i> [6 dorsal/extensor leg muscles/muscle groups: 4 (67%) seem to 'correspond' directly to forelimb muscles/muscle groups]
Long extensors	Extensor digitorum longus (m.IV and d.1) [Extensor digitorum] Tibialis anterior [Extensores antebrachii et carpi radialis] Fibularis longus (m.V and d.5) Fibularis brevis	Ex. digitorum longus (m.II-III, not to digitis) [Extensor digitorum] Tibialis anterior [Extensores antebrachii et carpi radialis] Fibularis longus Fibularis brevis	Extensor digitorum longus (m.I-III, sometimes also to m.IV) [Extensor digitorum] Tibialis anterior [Extensores antebrachii et carpi radialis] Fibularis longus Fibularis brevis	Ex. digitorum longus (to d.2-4) [Extensor digitorum] Tibialis anterior (tibialis cranialis) [Extensores antebrachii et carpi radialis] Fibularis longus Fibularis brevis
Short extensors	Extensores digitorum breves (3 muscles to d.2-4) [Extensores digitorum breves] Dorsometatarsales ('interossei dorsales'; 3 muscles to d.2-4) [Dorsometatarsales] Ab. et ex. digiti 1 ('ex.h.p.+ab.h.': d.1; ab.+ short ex. d.1) [Abductor pollicis longus]	Extensores digitorum breves (4 muscles to d.2-5 + part short ex. d.1) [Extensores digitorum breves] --- Ab. et ex. digiti 1 (to d.1; ab.+ part short ex. d.1) [Abductor pollicis longus]	Extensores digitorum breves (3 muscles to d.2-4) [Extensores digitorum breves] --- Ab. et ex. digiti 1 ('ex.h.l.': d.1; ab.+ short ex. d.1) [Abductor pollicis longus]	Extensores digitorum breves (3 muscles to d.2-4) [Extensores digitorum breves] --- Ab. et ex. digiti 1 ('ex.h.l.': d.1; ab.+ short ex. d.1) [Abductor pollicis longus]

The extensor digitorum longus, tibialis anterior, fibularis brevis, fibularis longus and extensores digitorum breves of birds clearly correspond to the muscles designated by similar names in humans. However, the “extensor hallucis longus” in birds is not homologous to the muscle designated with the same name in humans, because the last common ancestor of reptiles and mammals did not have a distinct extensor hallucis longus, and moreover the bird muscle corresponds to the abductor et extensor digiti 1 sensu the present work while the human extensor hallucis longus derives from the extensor digitorum longus. ab., abductor; ab.h, abductor hallucis; d., digits; ex., extensor; ex.h.l., extensor hallucis longus; ex.h.p., extensor hallucis proprius; m, metatarsals.

TABLE 20. Scheme illustrating the “clear topological correspondences” between the ventral/flexor leg and forearm muscles of adults of representative reptilian taxa (see caption of Table 13).

	<i>Trachemys scripta</i> [5 ventral/flexor leg muscles/muscle groups: 3 (60%) seem to 'correspond' directly to forelimb muscles/muscle groups]	<i>Timon lepidus</i> [6 ventral/flexor leg muscles/muscle groups: 4 (67%) seem to 'correspond' directly to forelimb muscles/muscle groups]	<i>Alligator mississippiensis</i> [7 ventral/flexor leg muscles/muscle groups: 4 (57%) seem to 'correspond' directly to forelimb muscles/muscle groups]	<i>Gallus gallus</i> [4 ventral/flexor leg muscles/muscle groups: 2 (50%) seem to 'correspond' directly to forelimb muscles/muscle groups]
Long flexors	--- (fl.cr. ta.ti. seems included in fl.ti.ex. and/or ga.in.) --- Gastrocnemius internus ('gastrocnemius'; 2 heads) Gastrocnemius externus ('f.d.l. sublimis') Flexor digitorum communis (to d.1-4) [Flexor digitorum longus] --- (but some turtles have a popliteus) Interosseus cruris [Pronator quadratus] Tibialis posterior ('pronator profundus') [Palmaris profundus 1]	--- (fl.cr. ta.ti. seems included in fl.ti.ex. and eventually ga.in.) --- Gastrocnemius internus ('femorotibial') Gastrocnemius externus ('femoral'; sup. and deep heads) Flexor digitorum longus (to d.1-5) [Flexor digitorum longus] Popliteus [Pronator accessorius] Interosseus cruris [Pronator quadratus] Tibialis posterior ('pronator profundus') [Palmaris profundus 1]	--- (fl.cr. ta.ti. seems included in fl.ti.ex. and/or ga.in.) Gastrocnemius plantaris ('plantaris') Gastrocnemius internus Gastrocnemius externus Flexor digitorum longus (d.1-4) [Flexor digitorum longus] Popliteus [Pronator teres] Interosseus cruris [Pronator quadratus] Tibialis posterior ('pronator profundus') [Flexor carpi radialis]	--- (fl.cr. ta.ti. seems included in ga.co. or lost) Gastrocnemius plantaris ('plantaris') Gastrocnemius (3 heads) --- Flexor digitorum longus ('f.d.l.+f.h.l.': to d.1-4) [Flexor digitorum longus] Popliteus [Pronator teres] --- ---

The flexor digitorum longus, popliteus and gastrocnemius of humans mainly correspond to at least part of the muscles designated by similar names in birds. However, the muscle that is usually named “plantaris” in birds is not homologous to the muscle designated with the same name in humans, because the last common ancestor of reptiles and mammals did not have a distinct plantaris muscle, hence we use a different name in birds. But, although the “plantaris” of birds does not directly correspond to the plantaris of humans, both the avian and human muscles derive from a similar anlage/ancestral muscle, i.e. from the gastrocnemius complex, hence the avian muscle is highlighted in bold. Regarding the avian “flexor hallucis longus,” although this structure and the extensor hallucis longus of humans are both derived from the flexor digitorum longus, the avian structure is simply a bundle of the flexor digitorum longus and not a separate muscle, in fact the last common ancestor of reptiles and mammals did not have a distinct flexor hallucis longus. d., digits; fl.cr.ta.ti., flexor cruris tarsi tibialis; f.d.l., flexor digitorum longus; f.h.l., flexor hallucis longus; fl.ti.ex., flexor tibialis externus; ga.co., gastrocnemius complex; ga.in., gastrocnemius internus; sup. superficial.

Taking into account these new data from anurans, turtles, crocodylians or birds, a conclusion with even broader and more important implications than Diogo et al.'s (2013) study can be reached: the number of muscles with “topological correspondences” in humans (N = 19) is not only higher than in anatomically more plesiomorphic, quadrupedal mammals such as rats (N = 16) and reptiles such as lizards (N = 14), but actually higher than in all other major non-urodelan groups examined in the present work (N anurans = 12; turtles = 13; crocodylians = 14; birds = 9). The number in humans is similar to that found in urodeles (N = 19; Fig. 2), which are remarkably plesiomorphic, both phylogenetically and anatomically (e.g. Owen, 1866; Humphry, 1872ab; Howell, 1936). Combined with the information provided in the previous section and the Results section,

these data strongly support the idea that evolutionary divergence and convergence/parallelism have both played crucial, sometimes counterbalancing roles in the evolution of the tetrapod FL and HL.

Regarding the strong similarity between the leg-foot and forearm-hand muscles in urodeles (“similarity bottleneck”: Figs. 2 and 3) and its bearing on the FL-HL homology hypothesis, it should be emphasized that the developmental changes associated with the “fins-limbs transition” that led to this similarity consist of phylogenetically derived co-option of a few similar genes (“genetic piracy” sensu Roth 1994; see also the recent review of Pavlicev and Wagner, 2012). It is now broadly accepted that the independent co-option of similar ancestral genes to form structures such as complex eyes in vertebrate and non-vertebrate animals (“deep

TABLE 21. Scheme illustrating the “clear topological correspondences” between the foot and hand muscles of adults of representative reptilian taxa (see caption of Table 1)

	<i>Trachemys scripta</i> [5 foot muscles/muscle groups: 5 (100%) seem to 'correspond' directly to forelimb muscles/muscle groups]	<i>Timon lepidus</i> [6 foot muscles/muscle groups: 6 (100%) seem to 'correspond' directly to forelimb muscles/muscle groups]	<i>Aligator mississippiensis</i> [6 foot muscles/muscle groups: 6 (100%) seem to 'correspond' directly to forelimb muscles/muscle groups]	<i>Gallus gallus</i> [5 foot muscles/muscle groups: 3 (60%) seem to 'correspond' directly to forelimb muscles/muscle groups]
limb/foot muscles	Flexores breves sup. (fl.di.com.sub.; 4 muscles to d.1-4) [Flexores breves superficiales]	Flexores breves sup. (3 muscles to d.1-3) [Flexores breves superficiales]	Flexores breves sup. (4 muscles to d.1-4) [Flexores breves superficiales]	Flexores breves sup. (f.p.p.II,III + f.p.II,III,IV; 5 muscles to d.2-4) [Flexores breves superficiales]
	Lumbricales (4 muscles to d.2-5) [Lumbricales]	Lumbricales (2 muscles to d.3-4) [Lumbricales]	Lumbricales (4 muscles, to d.1-4) [Lumbricales]	Lumbricales (2 muscles, to d.3-4)
	---	Abductor digiti minimi (1 muscle to m.V) [Abductor digiti minimi]	Abductor digiti minimi (mainly to m.IV) [Abductor digiti minimi]	Abductor digiti minimi (ab.di.IV; 1 muscle to d.4)
	Contrahentes pedis (p.i.p.; 4 muscles to d.1-4) [Contrahentes digitorum]	Contrahentes pedis (5 muscles to d.1-5) [Contrahentes digitorum]	Contrahentes pedis (at least 1 muscle to d.1) [Contrahentes digitorum]	Contrahentes pedis ('adductor digiti II'; 1 muscles to d.2) [Contrahentes digitorum]
	Flexores breves profundi (p.i.p.; 4 muscles to d.1-4) [Flexores breves profundi]	Flexores breves profundi (10 muscles to d.1-5) [Flexores breves profundi]	Flexores breves profundi (seemingly 8 muscles to d.1-4) [Flexores breves profundi]	Flexores breves profundi (Th.b.; 1 muscle to d.1) [Flexores breves profundi]
	Intermetatarsales (p.i.p.; 4 muscles connecting m.1-5) [Intermetatarsales]	Intermetatarsales (4 muscles connecting m.1-5) [Intermetatarsales]	Intermetatarsales (seemingly 3 muscles connecting m.1-4) [Intermetatarsales]	---

The flexores breves superficiales, lumbricales and abductor digiti minimi of birds clearly correspond to the muscles designated by similar names in humans. Regarding the avian “flexor hallucis brevis,” this muscle corresponds to the first flexor brevis profundis, so it does correspond to the flexor hallucis brevis of humans sensu the present work (i.e. to the structure usually designated as “medial head of the flexor hallucis longus” in human anatomy). However, in the last common ancestor of tetrapods and of amniotes this first flexor brevis profundis was clearly part of a group of muscles, the flexores breves profundi, and was not a distinct, separate, peculiar muscle as is the case in birds and humans, so the bird and human condition is the result of an evolutionary homoplasy (thence the bird muscle is highlighted in bold). ab.di.IV, abductor digiti IV; d., digits; fl.di.com.sub., flexor digitorum communis sublimis; f.h.b., flexor hallucis brevis; f.p.p.II,III + f.p. II,III,IV; flexor perforans et perforatus digiti II and III plus flexor perforatus digiti II, III and IV; m, metatarsals; p.”i.p.” part of “interossei plantares” sensu Walker 1973; sup., superficiales.

homology”) is a case of evolutionary parallelism and thus of homoplasy (e.g., Wilmer, 2003). Therefore, it would be very difficult to argue that the derived co-option of a few genes represents a case of FL-HL serial homology under the developmental concept of homology. This logic was recognized by Tabin (1992), who stated that the structures of the FL and HL of tetrapods evolved independently from the PEC and the PEL appendages, respectively, of fish. Tabin argued that this independent evolution is reflected in the significant differences between the FL and HL patterns (despite their general similarity) in fish prior to the evolution of limbs, as noted by Rackoff (1980). According to Tabin (1992), the similarities between the tetrapod FL and HL may be a direct consequence of the evolution of the limb buds by reorienting the expression of similar genes (e.g., *Hox-1* and *Hox-4*) along orthogonal axes, which have an effect on downstream target genes.

In fact, the musculature of the leg-foot in the first tetrapods might have been even more strikingly similar to the musculature of the forearm-hand than it is in anatomically plesiomorphic extant tetrapods such as salamanders. According to the comparative studies by authors such as McMurrich (1905) and Bardeen (1906) on extant salamanders such as *Ambystoma*, the distal (leg) portion of the ischioflexorius seems to correspond to an ancestral muscle flexor cruris et tarsi tibialis, while the femoral head of the flexor digitorum communis seems to correspond to an ancestral muscle flexor cruris et tarsi fibularis. If these correspondences are valid, all eight ventral forearm muscles of in the first tetrapods had a clear “topological equivalent” in the leg: the flexor antibrachii et carpi radialis and the flexor antibrachii et carpi ulnaris “corresponded” to the flexor cruris et tarsi tibialis and to the flexor cruris et tarsi fibularis, respectively. Therefore, the first tetrapods would have had at least 21 leg-foot muscles/muscle groups with “topological equivalents” in the forearm-hand, as opposed to 19 in salamanders (N.B., because the flexor cruris et tarsi tibialis and flexor cruris et tarsi fibularis are not present as separate structures in extant salamanders, only six

rather than eight of the individual salamander leg muscles have apparent “topological equivalents” in the forearm; Table 14). More importantly, the particularly strong ontogenetic factors/constraints, as well as the functional/topological factors/constraints (see below), involved in the “fins-limbs transition” may thus have produced dorsal forearm musculature in early tetrapods that was strikingly similar not only to the dorsal leg musculature, but also to the ventral forearm and leg musculature (dorso-ventral symmetry). The authors are currently undertaking a developmental study in axolotls and other tetrapods to test this hypothesis.

Even the co-option of similar genes during the “fins-limbs transition” is not sufficient to explain the striking similarity between the leg-foot and forearm-hand muscles of phylogenetically and anatomically derived tetrapods such as our bipedal species, *H. sapiens* (Fig. 2). Many of the 19 FL-HL muscles/muscle groups in modern humans with apparent “topological equivalents” were undoubtedly acquired independently during the evolutionary history of primates (Diogo and Wood, 2012; Diogo et al., 2013). Such “similarity bottlenecks” have also occurred during the evolutionary history of other derived tetrapod and even non-tetrapod clades; e.g., the various PEL muscles of plesiomorphic teleosts were derived independently from the various PEC muscles of these fish but are topologically very similar to them (e.g., Winterbottom, 1974; Diogo and Abdala, 2010). Additional examples of homoplasy between FL and HL bones can be seen in horses and *Plesiosaurus* (e.g., Owen, 1849). In addition to ontogenetic constraints, the “similarity bottlenecks” leading to such derived clades (Fig. 2) are clearly due to topological and functional constraints. For instance, the only functional configuration for an abductor hallucis/pollicis brevis is a muscle that lies tibial/radial to the first digit of the foot/hand and inserts onto the tibial/radial side of this digit. Both muscles were homoplastically acquired during tetrapod evolution (Table 15).

The fact that topologically similar leg-foot and forearm-hand muscles in such taxa do not develop from similar anlagen (Tables 13–15) is a crucial point in

support of the idea that ontogenetic constraints are not sufficient to explain the “similarity bottlenecks” leading to derived taxa such as modern humans (Fig. 2). For instance, the extensor pollicis longus and extensor hallucis longus in modern humans are remarkably similar topologically, but the former derives from the anlage of the short extensors of the hand, while the latter derives from the anlage of the long extensors of the leg (Diogo and Wood, 2012; Table 15). Moreover, many of these muscles, or their subdivisions, formed at different geological times and/or phylogenetic nodes. For example, the adductor hallucis and adductor pollicis in modern humans are particularly similar to each other because they have well-differentiated transverse and oblique heads. However, unlike the adductor hallucis heads, which are well differentiated in phylogenetically plesiomorphic primates such as lemurs, the adductor pollicis heads only became well differentiated in the much more derived node leading to catarrhines (old world monkeys + hominoids; for more examples see Diogo et al., 2013). Several additional examples of similar FL-HL muscles derived from different anlages and/or appearing at different geological times are shown in Tables 13 to 21 and described in the Results section.

CONCLUSIONS

In summary, evolutionary divergences in the history of tetrapods have produced differences between the FL and HL musculature which are not seen in anatomically plesiomorphic tetrapods such as urodeles. However, there are also cases of evolutionary parallelism/convergence leading to subsequent “similarity bottlenecks” between the FL and HL in more derived taxa (Tables 13–15). The striking similarity of many PEC and PEL muscles found in gnathostome taxa such as modern humans and teleost fishes is undoubtedly the result of homoplasy due to a complex interplay between ontogenetic, topological, functional and even phylogenetic (Diogo et al., 2013) constraints/factors, and not of serial homology. We hope that the new data and the discussion provided in this article will lead to deconstruction of the serial homology hypothesis and promote more integrative studies on the puzzling and fascinating evolutionary history of the paired appendages in all its complexity, including the importance of homoplasy and constraints, under a new paradigm.

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