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Is evolutionary biology becoming too politically correct? A reflection on *the scala naturae*, phylogenetically basal clades, anatomically plesiomorphic taxa, and ‘lower’ animals

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ABSTRACT

The notion of *scala naturae* dates back to thinkers such as Aristotle, who placed plants below animals and ranked the latter along a graded scale of complexity from ‘lower’ to ‘higher’ animals, such as humans. In the last decades, evolutionary biologists have tended to move from one extreme (i.e. the idea of *scala naturae* or the existence of a general evolutionary trend in complexity from ‘lower’ to ‘higher’ taxa, with *Homo sapiens* as the end stage) to the other, opposite, extreme (i.e. to avoid using terms such as ‘phylogenetically basal’ and ‘anatomically plesiomorphic’ taxa, which are seen as the undesired vestige of old teleological theories). The latter view tries to avoid any possible connotations with the original anthropocentric idea of a *scala naturae* crowned by man and, in that sense, it can be regarded as a more politically correct view. In the past years and months there has been renewed interest in these topics, which have been discussed in various papers and monographs that tend to subscribe, in general, to the points defended in the more politically correct view. Importantly, most evolutionary and phylogenetic studies of tetrapods and other vertebrates, and therefore most discussions on the *scala naturae* and related issues have been based on hard tissue and, more recently, on molecular data. Here we provide the first discussion of these topics based on a comparative myological study of all the major vertebrate clades and of myological cladistic and Bayesian phylogenetic analyses of bony fish and tetrapods, including Primates. We specifically (i) contradict the notions of a *scala naturae* or evolutionary progressive trends leading to more complexity in ‘higher’ animals and culminating in *Homo sapiens*, and (ii) stress that the refutation of these old notions does not necessarily mean that one should not keep using the terms ‘phylogenetically basal’ and particularly ‘anatomically plesiomorphic’ to refer to groups such as the urodeles within the Tetrapoda, or the strepsirrhines and lemurs within the Primates, for instance. This review will contribute to improving our understanding of these broad evolutionary issues and of the evolution of the vertebrate Bauplans, and hopefully will stimulate future phylogenetic, evolutionary and developmental studies of these clades.

Key words: basal, evolution, development, derived, humans, muscles, plesiomorphic, phylogeny, salamanders, tetrapods.

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I. INTRODUCTION

A series of papers have recently warned researchers and educators in the field of evolutionary biology about the persistent use of terms such as ‘lower’ and ‘higher’ taxa in professional papers and textbooks (Krell & Cranston, 2004; Baum, Smith & Donovan, 2005; Crisp & Cook, 2005; Nee, 2005; Gregory, 2008; Omland, Cook & Crisp, 2008; Johnson, Lahti & Blumstein, 2012; Moore, 2013; Rigato & Minelli, 2013). According to these authors, the use of such terms is symptomatic of a misconception about evolution as a progressive process towards higher levels of complexity, culminating in our own species, *Homo sapiens*. Classifications of living beings based on levels of complexity can be traced back to the ancient Greeks. For example, Aristotle placed plants below animals due to the ability of the latter to move, which would be regarded as a complex behaviour; he also ranked animals along a graded scale of complexity based on the presence/absence of blood and type of reproduction (e.g. Bonner, 1988). Other versions of this lineal, progressive classification or *scala naturae* – ‘ladder of nature’ – also included the non-living realm of minerals at the lower rung; in its religious version called *The Great Chain of Being*, God, at the top position, represented the culmination point of this progression towards perfection (Lovejoy, 1936). Religious thought, and particularly *The Great Chain of Being*, is deeply related to the biological notion of a *scala naturae* because humans occupied a unique position on the *Chain of Being*, between angels and ‘animals’; like angels, humans were seen as spiritual beings, but unlike angels, human souls were seen as bounded to a physical body (Lovejoy, 1936).

The idea that complexity has, in some way, increased over the course of evolution has been shared by most evolutionists, from Lamarck to 20th Century scientists, including Darwin (McShea, 1991, 1996; Richards, 1992). According to McShea (1991, 1996), however, this shared perception about an overall progressive evolutionary trend towards higher complexity has been based more on intuition than on robust empirical results. An illustrative example supporting McShea’s (1991, 1996) view is given in the book *The evolution of complexity*, in which Bonner (1988, p. 5) stated that it is clear that ‘the most complex organism of all is our own kind’ without however providing any kind of empirical data to corroborate this statement. The only definition of phenotypic complexity given in the whole book is that more complex organisms are those with a greater number of different types of cells and/or a greater number of interactions between the cells. But the only information that Bonner (1988) provides in the book about these numbers is simply a rough estimate that ‘Vertebrates’ have more than 120 types of cells (his fig. 8); he never provides the specific numbers for any vertebrate animal, including humans. Furthermore,

studies of evolutionary trends have been biased towards those taxa and organismal substructures on which a trend was foreseeable prior to data analysis (McShea, 1991, 1996; Gould, 2002). Gould (2002) referred to this sampling bias as the *Cordelia’s dilemma*. In Shakespeare’s play *King Lear*, the king wants to retire from power and decides to divide his realm among his three daughters. He tells them that he will give the largest part to the one who demonstrates the best love for him. Two of his daughters, Regan and Goneril, feign to love him more than anyone, when they really view him as a foolish man. Cordelia, uncomfortable with her sisters’ behaviour, decides to say nothing, even if she feels true love for her father. The king interprets Cordelia’s silence as indifference and disinherits her. In Gould’s (2002) analogy, taxa and organismal substructures that do not show a foreseeable evolutionary trend – they are ‘silent’ to researchers’ eyes – would be sidestepped. This sampling bias would give the impression that general evolutionary trends are more abundant than they probably are (see, e.g. Diogo, 2006, for some examples).

The persistence of progressionist language in professional papers and textbooks has been at least partially attributed to problems with the interpretation of phylogenetic trees. According to various authors, one of the major problems consists in reading the tree from left to right at the tips, that is, the tree is interpreted as a lineal pathway of evolutionary change similar to a *ladder of progress* or *scala naturae* (Crisp & Cook, 2005; Omland *et al.*, 2008). According to them, this interpretation leads to the incorrect idea that extant taxa at the left of the tree are the ancestors of extant taxa located at the right, while in reality the time arrow in phylogenetic trees does not run horizontally, from left to right, but vertically, from the root to the tips. Therefore, these authors have argued that it is not correct to refer to any extant taxa (i.e. a terminal node) as ‘phylogenetically basal’ because all extant taxa have survived to the present day and evolved in their own peculiar and unique way. In such a view, the term ‘phylogenetically basal’ taxon would be applicable only to the hypothetical reconstructions at the internal nodes (Crisp & Cook, 2005; Omland *et al.*, 2008). Authors such as Casane & Laurenti (2013) have argued that, by taking into account that all lineages continue to evolve, no extant species would display, strictly speaking, the plesiomorphic condition of a specific trait, although it is known that the evolutionary rates of some anatomical features have slowed down in some lineages (we are aware that, by definition, the term ‘plesiomorphic’ refers to ‘primitive shape’, i.e. to anatomy; however, because evolutionary biologists now commonly use terms such as ‘genetically plesiomorphic’ or ‘plesiomorphic behaviour’, we prefer to use the term ‘anatomically plesiomorphic’ throughout this paper). As a consequence, it has been argued that comparative studies of extant species

cannot provide convincing support for the existence of evolutionary trends or be used as models for the study of the origin and evolution of major clades (e.g. Gregory, 2008).

The renewed interest in these issues is also reflected in the recent publication of a series of books, including *Randomness in evolution* (Bonner, 2013), *Evolution without Darwinism* (Butler, 2012), *Evolution - the extended synthesis* (Pigliucci & Muller, 2010), *Forms of becoming* (Minelli, 2009), *Evolution - a developmental approach* (Arthur, 2011), *Modular evolution - how natural selection produces biological complexity* (Vinicius, 2012), and *Not by design: retiring Darwin's watchmaker* (Reiss, 2009), among others. The conflicting ideas about the existence of an evolutionary trend in complexity that has pervaded most of the history of evolutionary thought is still palpable in, for example, the contrasting views presented by the same author at different periods. For instance, in an older book, *The evolution of complexity* (Bonner, 1988) the author explicitly defended the existence of an increase of complexity from 'lower' to 'higher' organisms, the 'highest' of all being *Homo sapiens*, an increase which had been driven presumably by natural selection; in a more recent book, *Randomness in evolution* (Bonner, 2013), the author stresses instead the crucial role played by randomness in biological evolution (Bonner, 1988, 2013) and the possibility that evolutionary trends are passive or non-driven. Butler (2012) also provides an interesting review of the change of ideas that has occurred in the last decades and of some key researchers that have been crucial in that process. This change of ideas and some of the other issues addressed in the present paper have also been discussed in an elegant book by Ruse (2003) *Darwin and design - does evolution have a purpose?*.

By trying to avoid the old progressionist taint of some evolutionary and phylogenetic terminology (associated with the notions of *scala naturae* and 'progress'), evolutionary biologists are now increasingly tending to go to the other extreme (i.e. to reject the use of terms such as 'phylogenetically basal' and 'anatomically plesiomorphic' taxa). In our opinion, this latter view is probably becoming too politically correct as it seems to suggest that one can no longer use terms such as 'anatomically plesiomorphic' to refer, for instance, to coelacanths within sarcopterygians, salamanders within tetrapods or lemurs within primates [reviewed by Diogo & Wood (2012a); see also Casane & Laurenti's (2013) recent paper 'Why coelacanths are not living fossils']. It is argued that living taxa are all the same age (there are not 'phylogenetically basal' living taxa) and each has evolved in its own peculiar way, departing, to some extent, from the ancestral condition (there are not 'anatomically plesiomorphic' living taxa; see e.g. Casane & Laurenti, 2013). These ideas are especially problematic for comparative, evolutionary and developmental studies of soft tissues, for instance, due to the scarcity of

fossil records on these tissues (Diogo & Abdala, 2010). In fact, it is important to note that most evolutionary and phylogenetic studies of tetrapods and other vertebrates, and therefore most discussions on the *scala naturae* and the other issues addressed in the present review have been themselves based on hard tissue and, more recently, on molecular data. The most original aspect of the present review is that we provide the first discussion of these issues based on the results of a detailed comparative myological study of all the major vertebrate clades and of myological cladistic and Bayesian phylogenetic analyses of bony fish and tetrapods, including Primates. We specifically: (i) contradict the notions of a *scala naturae* or evolutionary progressive trends leading to more complexity in 'higher' animals and culminating in *Homo sapiens*; and (ii) stress that the refutation of the old notion does not necessarily mean that one should avoid using the terms 'phylogenetically basal' and, particularly, 'anatomically plesiomorphic' to refer to groups such as the lemurs within the strepsirrhines and the Primates, or the urodeles within the Tetrapoda, for example.

II. COMPARATIVE ANATOMY, PHYLOGENY, MUSCLES AND ANATOMICALLY PLESIOMORPHIC TAXA

To address the scarcity of phylogenetic studies of vertebrate taxa including myological data, Diogo (2004a,b) used 91 myological and 303 osteological characters to reconstruct the higher level phylogeny of catfish (Siluriformes), and Diogo (2007) used a total of 356 skeletal and myological characters to study the phylogeny of 80 extant and fossil osteichthyan taxa (bony 'fish' plus tetrapods). More recently, Diogo & Wood (2011, 2012a,b, 2013) used the information obtained from dissections of the head, neck, pectoral and upper limb muscles of representative taxa of each major extant primate group (see Table 3), and of the outgroups Glires, Dermoptera and Scandentia, in both parsimony and Bayesian cladistic analyses that included a total of 166 myological characters. The most parsimonious tree obtained from these analyses was essentially similar to the molecular trees obtained recently by Fabre, Rodrigues & Douzery (2009), Arnold, Matthews & Nunn (2010), and Perelman *et al.* (2011). The myological phylogenetic works of Diogo & Wood (2011, 2012a,b, 2013) are part of a long-term project to investigate the comparative anatomy, homologies, evolution, development and phylogeny of the striated muscles of all major groups of vertebrates (Diogo, 2007; Diogo & Abdala, 2007, 2010; Diogo *et al.*, 2008, 2009a,b; Abdala & Diogo, 2010). The phylogenetic and anatomical results obtained so far have revealed that muscle characters are particularly useful to generate phylogenies and to study and discuss broad evolutionary topics (see recent review of Diogo & Wood, 2013).

These studies have provided new data to explore the idea of a *scala naturae* and the notions of ‘phylogenetically basal’, ‘anatomically plesiomorphic’ and ‘lower’/‘higher’ taxa. For instance, it is possible to compare the number and identity of the muscles and muscle bundles found in each extant taxon from a certain clade (Tables 1–3) and found in the last common ancestor (LCA) of that clade (e.g. Tables 1 and 2; Fig. 1). Furthermore, these studies also allow comparison of the number of muscles found in each extant taxon of a clade with the number of phylogenetic evolutionary steps (including original acquisitions, losses and reversions) that were accumulated from the origin of that clade to the respective extant taxon [e.g. from the origin of primates to each of the primate genera listed in Table 3; see Section III and Diogo & Wood (2011, 2012*a*, 2013) for details regarding methodology]. In order to discuss the major evolutionary topics that are the focus of this review, we will therefore provide here, for the first time, a detailed comparison of the number and identity of the head, neck, pectoral and upper limb muscles of various extant tetrapod taxa including salamanders, frogs, lizards, monotremes, lemurs and modern humans, and of the LCA of all extant tetrapods, amniotes, mammals and primates (Tables 1 and 2). These muscles (head, neck, pectoral and upper limb) are those included in our previous cladistic analyses, and therefore are those for which we have detailed information about the condition found in the LCA of tetrapods, amniotes, mammals and primates. This methodology avoids circular reasoning because, for instance, whether one considers *a priori* that salamanders are anatomically more plesiomorphic than frogs and than other extant tetrapods regarding head musculature has no impact on the definition of the features of the LCA of extant tetrapods. This is because those features are instead defined by the empirical results of our previous cladistic analyses, which used the outgroup method to code polarity/optimize the evolution of the character states (in this specific example, interactively taking into account the condition found in those taxa that, also according to the cladistic analyses, appear as the closest living relatives of amniotes, i.e. amphibians, including anurans, urodeles and caecilians). The information given in Tables 1 and 2 allows us to report the first assessment of the specific percentages regarding: (i) the number of muscles of each of these LCAs that has been kept in each of the extant taxa analysed; and (ii) the number of ancestral muscles *versus* the total number of muscles found in each of these extant taxa.

For instance, as can be seen in Table 1, the LCA of all extant tetrapods (LCAT) had 39 pectoral and forelimb muscles/muscle groups [m/mg; based on comparative data and phylogenetic reconstructions provided by Diogo (2007), Diogo & Abdala (2010), Diogo & Tanaka (2012) and Diogo *et al.* (2013*a*)]. Note that in order to facilitate comparisons among different tetrapod taxa,

we group serial muscles going to different digits, e.g. the flexores superficiales, in a muscle group that occupies a single cell in Table 1). The neotenic salamander *Ambystoma mexicanum* (Amphibia: Urodela) or axolotl has 33 pectoral and forelimb m/mg, of which 31 (94%) were present in the LCAT, i.e. it keeps 31 (79%) of the ancestral 39 m/mg. By contrast, the frog *Rana pipiens* (Amphibia: Anura) has 41 pectoral and forelimb m/mg, of which 34 (83%) were present in the LCAT, keeping 34 (87%) of the ancestral 39 m/mg. It is therefore clear that the pectoral and forelimb muscles of an axolotl are in general much more similar to those of the LCAT than are those of a frog such as *Rana pipiens*: 94% of the m/mg found currently in axolotls were present in the LCAT *versus* 83% in the frog. To maintain coherence and objectivity throughout this paper, we will use $\geq 90\%$ similarity with a certain LCA as the criterion for a taxon to be considered as a good model for that respective LCA. This is principally due to the fact that, during the evolutionary events that led to the configuration now found in axolotls, only two new m/mg, not present in the LCAT, were acquired (flexores digitorum minimi and interphalangei). By contrast, seven new m/mg were acquired during the evolutionary events leading to *Rana pipiens* [the flexores digitorum minimi and interphalangei acquired before the origin of anurans, plus the rhomboideus occipitalis, opercularis, columellaris, flexor accessorius (due to the fusion of the flexor accessorius medialis and lateralis), and abductor pollicis longus (due to separation between short abductor and short extensor of digit 1), acquired during anuran evolution]. Importantly, the overall configuration of the pectoral and forelimb m/mg found in some other urodeles is even more similar to that of the LCAT than that in axolotls (see Table 1). This is due to the fact that all the 8 m/mg that were present in the LCAT but not found in axolotls have been described in some other urodeles, with the exception of the levator claviculae and serratus anterior (Diogo & Abdala, 2010). That is, the LCA of extant urodeles very likely had at least 37 (95%) of the 39 pectoral and forelimb m/mg present in the LCAT, their absence in the axolotl being a derived characteristic due to recent evolutionary change likely associated with their neotenic condition. This idea is supported by the facts that: (i) muscles such as the epitrochleoanconeus, anconeus, pronator teres, brachioradialis and dorsometacarpales usually differentiate relatively late during tetrapod limb development (e.g. Bardeen, 1906; Diogo & Ziermann, 2014), and (ii) at least some of these muscles are in fact found in non-neotenic salamanders such as terrestrial species of the genus *Salamandra* (e.g. Straus, 1941*a,b*). In summary, at least in terms of the myology of their pectoral region and forelimb, urodeles are a good model to discuss tetrapod evolution and can be effectively designated as ‘anatomically plesiomorphic’ tetrapods (see Section III). In the future we hope to be able to add more urodele species, as well as more

Table 1. Scheme illustrating the evolution and homologies of the pectoral and forelimb muscles of adults of representative tetrapod taxa (based on Diogo & Abdala, 2010; Diogo & Wood, 2011, 2012a; Diogo & Tanaka, 2012); for taxonomy and further details, see text

	<i>Ambystoma mexicanum</i> [33 m/mg, 31 (94%) of them = LCAT, keeping 31/39 (79%) m/mg of LCAT; but some urodeles have all muscles of LCAT except the Serratus anterior and Levator scapulae, thus keeping 37/39 (95%) of LCAT]	<i>Rana pipiens</i> [41 m/mg, 34 (83%) of them = LCAT, keeping 34/39 (87%) of LCAT]	<i>Timon lepidus</i> [37 m/mg, 28 (76%) of them = LCAT, and 36 (97%) = LCAM, keeping 28/39 (72%) of LCAT and 36/42 (86%) of LCAM]	<i>Ornithorhynchus anatinus</i> [45 m/mg, 25 (56%) of them = LCAT, 33 (73%) = LCAM, and 45 (100%) = LCAM, keeping 25/39 (64%) of LCAT, 34/42 (81%) of LCAM, and 45/50 (90%) of LCAM]	<i>Lemur catta</i> [55 m/mg, 27 (49%) of them = LCAT, 33 (60%) = LCAM, 45 (82%) = LCAM, and 55 (100%) = LCAM, keeping 27/39 (69%) of LCAT, 33/42 (79%) of LCAM, 45/50 (90%) of LCAM, and 55/55 (100%) = LCAP]	<i>Homo sapiens</i> [50 m/mg, 21 (42%) of them = LCAT, 27 (54%) = LCAM, 37 (74%) = LCAM, and 45 (90%) = LCAP, keeping 21/39 (54%) of LCAT, 27/42 (64%) of LCAM, 37/50 (74%) of LCAM, and 45/55 (82%) = LCAP]
Serratus anterior + rhomboideus	Serratus anterior + rhomboideus	Serratus anterior + rhomboideus	Serratus anterior + rhomboideus	Serratus anterior + rhomboideus	Serratus anterior + rhomboideus	Serratus anterior + rhomboideus
Levator scapulae + levator clavicular	Levator scapulae + levator clavicular	Levator scapulae + levator clavicular	Levator scapulae + levator clavicular	Levator scapulae + levator clavicular	Levator scapulae + levator clavicular	Levator scapulae minor
Pectoralis	Pectoralis	Pectoralis	Pectoralis	Pectoralis major + pectoralis minor + panniculus carnosus (part)	Pectoralis major + pectoralis minor + panniculus carnosus (part)	Pectoralis major + pectoralis minor
Supratoracoides	Supratoracoides	Supratoracoides	Supratoracoides	Supratoracoides	Supratoracoides	Subclavius
Deltoides scapularis	Deltoides scapularis	Deltoides scapularis	Deltoides scapularis	Deltoides scapularis + teres minor	Deltoides scapularis + teres minor	Deltoides scapularis + teres minor
Procoraco-humeralis	Procoraco-humeralis	Procoraco-humeralis	Procoraco-humeralis anterior	Deltoides clavicularis + scapulo-humeralis anterior	Deltoides clavicularis	Deltoides (part)
Subcoraco-capularis	Subcoraco-capularis	Subcoraco-capularis	Subcoraco-capularis	Subscapularis + teres major	Subscapularis + teres major	Subscapularis + teres major
Latissimus dorsi Triceps brachii	Latissimus dorsi Triceps brachii	Latissimus dorsi Triceps brachii	Latissimus dorsi Triceps brachii	Latissimus dorsi Triceps brachii + dorsoepitrochlearis trochlearis	Latissimus dorsi Triceps brachii + dorsoepitrochlearis chlearis	Latissimus dorsi Triceps brachii
Humeroante-brachialis	Humeroante-brachialis	Brachialis	Brachialis	Brachialis	Brachialis	Brachialis
Coracoradialis	Coracoradialis	Biceps brachii	Biceps brachii	Biceps brachii	Biceps brachii	Biceps brachii
Coracobrachialis	Coracobrachialis	Coracobrachialis	Coracobrachialis	Coracobrachialis	Coracobrachialis	Coracobrachialis

Axial: pectoral girdle

Appendicular: pectoral girdle and arm

Table 1. Continued

	<i>Ambystoma mexicanum</i> [33 m/mg, 31 (94%) of them = LCAT, keeping 31/39 (79%) m/mg of LCAT; but some urodeles have all muscles of LCAT except the Serratus anterior, and Levator scapulae, thus keeping 37/39 (95%) of LCAT]	<i>Rana lipitians</i> [41 m/mg, 34 (83%) of them = LCAT, keeping 34/39 (87%) of LCAT]	<i>Timon lepidus</i> [37 m/mg, 28 (76%) of them = LCAT, and 36 (97%) = LCAA, keeping 28/39 (72%) of LCAT and 36/42 (86%) of LCAA]	<i>Omiithorhynchus anatinus</i> [45 m/mg, 25 (56%) of them = LCAT, 33 (73%) = LCAA, and 45 (100%) = LCAM, keeping 25/39 (64%) of LCAT, 34/42 (81%) of LCAA, and 45/50 (90%) of LCAM]	<i>Lemur catta</i> [55 m/mg, 27 (49%) of them = LCAT, 33 (60%) = LCAA, 45 (82%) = LCAM, and 55 (100%) = LCAP, keeping 27/39 (69%) of LCAT, 33/42 (79%) of LCAA, 45/50 (90%) of LCAM, and 55/55 (100%) = LCAP]	<i>Homo sapiens</i> [50 m/mg, 21 (42%) of them = LCAT, 27 (54%) = LCAA, 37 (74%) = LCAM, and 45 (90%) = LCAP, keeping 21/39 (54%) of LCAT, 27/42 (64%) of LCAA, 37/50 (74%) of LCAM, and 45/55 (82%) = LCAP]
LCAT (39 m/mg)		LCAA (42 m/mg)		LCAM (50 m/mg)	LCAP (55 m/mg)	
Palmaris profundus 1	—	Palmaris profundus 1	Palmaris profundus 1	—	—	—
Pronator quadratus	Pronator quadratus	Pronator quadratus	Pronator quadratus + accessorius	Pronator quadratus	Pronator quadratus	Pronator quadratus
Contrahentium	Contrahentium	—	—	—	—	—
Flexor accessorius lateralis	caput longum Flexor accessorius lateralis	Contrahentium caput longum Flexor accessorius lateralis	—	—	—	—
Flexor accessorius medialis	Flexor accessorius medialis	—	—	—	—	—
Flexor digitorum communis	Flexor digitorum communis	Flexor digitorum communis	Flexor digitorum longus	Flexor digitorum longus	Flexor digitorum profundus + flexor digitorum superficialis (part) + palmaris longus	Flexor digitorum profundus + flexor digitorum superficialis (part) + flexor pollicis longus + palmaris longus
Flexor carpi ulnaris + epitrochleoconeus	Flexor carpi ulnaris + epitrochleoconeus found in other urodeles	Flexor carpi ulnaris + epitrochleoconeus	Flexor carpi ulnaris + epitrochleoconeus	Flexor carpi ulnaris + epitrochleoconeus	Flexor carpi ulnaris + epitrochleoconeus	Flexor carpi ulnaris
Flexor carpi radialis + pronator teres	Flexor carpi radialis + pronator teres (but pronator teres found in other urodeles)	Flexor carpi radialis + pronator teres	Flexor carpi radialis + pronator teres	Flexor carpi radialis + pronator teres	Flexor carpi radialis + pronator teres	Flexor carpi radialis + pronator teres

Appendicular: ventral forearm

Table 1. Continued

	<i>Amphystoma mexicanum</i> [33 m/mg, 31 (94%) of them = LCAT, keeping 31/39 (79%) m/mg of LCAT; but some urodeles have all muscles of LCAT except the Serratus anterior and Levator scapulae, thus keeping 37/39 (95%) of LCAT]	<i>Rana pipiens</i> [41 m/mg, 34 (83%) of them = LCAT, keeping 34/39 (87%) of LCAT]	<i>Timon lepidus</i> [37 m/mg, 28 (76%) of them = LCAT and keeping 28/39 (72%) of LCAT and 36/42 (86%) of LCAA]	<i>Ornithorhynchus anatinus</i> [45 m/mg, 25 (56%) of them = LCAT, 33 (73%) = LCAA and 45 (100%) = LCAM, keeping 25/39 (64%) of LCAT, 34/42 (81%) of LCAA, and 45/50 (90%) of LCAM]	<i>Lomur catta</i> [55 m/mg, 27 (49%) of them = LCAT, 33 (60%) = LCAM, 45 (82%) = LCAM, and 55 (100%) = LCAP, keeping 27/39 (69%) of LCAT, 33/42 (79%) of LCAM, 45/50 (90%) of LCAM, and 55/55 (100%) = LCAP]	<i>Homo sapiens</i> [50 m/mg, 21 (42%) of them = LCAT, 27 (54%) = LCAM, 37 (74%) = LCAM, and 45 (90%) = LCAP, keeping 21/39 (54%) of LCAT, 27/42 (64%) of LCAM, 37/50 (74%) of LCAM, and 45/55 (82%) = LCAP]
Flexores breves superficiales	Flexores breves superficiales	Flexores breves superficiales	Flexores breves superficiales	Flexores digitorum superficiales (tendons)	Flexores digitorum superficiales (part) + palmaris brevis	Flexores digitorum superficiales (part) + palmaris brevis
Lumbricales	Lumbricales	Lumbricales	Lumbricales	Lumbricales	Lumbricales	Lumbricales
Contrahentes digitorum	Contrahentes digitorum	Contrahentes digitorum	Contrahentes digitorum + adductor pollicis	Adductor pollicis	Contrahentes digitorum + adductor pollicis	Adductor pollicis + volaris primus of Henle'
Flexores breves profundi	Flexores breves profundi	Flexores breves profundi	Flexores breves profundi	Flexores breves profundi	Flexores breves profundi 2 + flexor pollicis brevis + opponens pollicis + flexor digiti minimi brevis + opponens digiti minimi + flexores breves profundi	Flexores breves profundi 2 + flexor pollicis brevis + opponens pollicis + flexor digiti minimi brevis + opponens digiti minimi + interossei (part)
Flexores digitorum minimi	Flexores digitorum minimi	Flexores digitorum minimi	Flexores digitorum minimi	Flexores digitorum minimi	Flexores digitorum minimi	Flexores digitorum minimi
Interphalangei	Interphalangei	Interphalangei	Abductor pollicis brevis	Abductor pollicis brevis	Abductor pollicis brevis	Abductor pollicis brevis
Abductor digiti minimi	Abductor digiti minimi	Abductor digiti minimi	Abductor digiti minimi	Abductor digiti minimi	Abductor digiti minimi	Abductor digiti minimi
Intermetacarpales	Intermetacarpales	Intermetacarpales	Intermetacarpales	Intermetacarpales	Intermetacarpales	Intermetacarpales
Dorsometacarpales	Dorsometacarpales	Dorsometacarpales	Dorsometacarpales	—	—	—
— (but dorsometacarpales found in some urodeles)	— (but dorsometacarpales found in some urodeles)	— (but dorsometacarpales found in some urodeles)	— (but dorsometacarpales found in some urodeles)	—	—	—

Appendicular: ventral and dorsal hand

Table 2. Continued

	<i>Ambytostoma mexicanum</i> [20m/mg, 17 (85%) of them = LCAT, keeping 17/18 (94%) m/mg of LCAT]	<i>Rana pipiens</i> [19 m/mg, 17 (89%) of them = LCAT, keeping 17/18 (94%) of LCAT]	<i>Timon lepidus</i> [25 m/mg, 17 (68%) of them = LCAT and 20 (80%) = LCAA, keeping 17/18 (94%) of LCAT and 20/20 (100%) of LCAA]	LCAM (32 m/mg)	<i>Omitotherhynchus anatinus</i> [31 m/mg, 6 (19%) of them = LCAT, 7 (23%) = LCAA, and 30 (97%) = LCAM, keeping 6/18 (33%) of LCAT, 7/20 (35%) of LCAA, and 30/32 (94%) of LCAM]	LCAP (39 m/mg)	<i>Lemur catta</i> [35 m/mg, 6 (17%) of them = LCAT, 9 (26%) = LCAA, 22 (63%) = LCAM, and 35 (100%) = LCAP, keeping 6/18 (33%) of LCAT, 9/20 (45%) of LCAA, 22/32 (69%) of LCAM, and 35/39 (90%) = LCAP]	<i>Homo sapiens</i> [39 m/mg, 6 (15%) of them = LCAT, 9 (23%) = LCAA, 21 (54%) = LCAM, and 36 (92%) = LCAP, keeping 6/18 (33%) of LCAT, 9/20 (45%) of LCAA, 21/32 (66%) of LCAM, and 36/39 (92%) = LCAP]
LCAT (18 m/mg)	Geniohyoideus Genioglossus Hyoglossus	Geniohyoideus Genioglossus Hyoglossus	Geniohyoideus Genioglossus Hyoglossus	Geniohyoideus Genioglossus Hyoglossus	Geniohyoideus Genioglossus Hyoglossus + styloglossus + palatoglossus	Geniohyoideus Genioglossus Hyoglossus + styloglossus + palatoglossus	Geniohyoideus Genioglossus Hyoglossus + styloglossus + palatoglossus	
—	—	Intrinsic muscles of the tongue	Intrinsic muscles of the tongue	Intrinsic muscles of the tongue	Intrinsic muscles of the tongue	Intrinsic muscles of the tongue	Intrinsic muscles of the tongue	
Sternohyoideus + omohyoideus	Interradialis Sternohyoideus + omohyoideus	Sternohyoideus + omohyoideus	Sternohyoideus + omohyoideus	Sternohyoideus + omohyoideus + sternothyroideus	Sternohyoideus + omohyoideus + sternothyroideus + thyrohyoideus	Sternohyoideus + omohyoideus + sternothyroideus + thyrohyoideus	Sternohyoideus + omohyoideus + sternothyroideus + thyrohyoideus	

LCA, last common ancestor; LCAA, last common ancestor of amniotes; LCAM, last common ancestor of mammals; LCAP, last common ancestor of tetrapods; m/mg, muscle/muscle groups.

Table 3. Table summarizing the total number of mandibular, hyoid (not including the small facial, extrinsic muscles of the ear), branchial, hypobranchial, pectoral, arm, forearm and hand muscles in adults of the primate genera (based on Diogo & Wood, 2011, 2012a,b)

	<i>Lemur</i>	<i>Propithecus</i>	<i>Loris</i>	<i>Nycticebus</i>	<i>Tarsius</i>	<i>Ptilocercus</i>	<i>Aotus</i>	<i>Saimiri</i>	<i>Callithrix</i>	<i>Cebus</i>	<i>Cercopithecus</i>	<i>Papio</i>	<i>Macaca</i>	<i>Haplorhina</i>	<i>Pongo</i>	<i>Gorilla</i>	<i>Pan</i>	<i>Homo</i>
Mandibular muscles	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
Hyoid muscles (not extrinsic ear)	25	24	24–26	26	24	22	23	21	22	24–25	26–27	25–26	26	26	26	26	26	27
Branchial muscles	14–16	14–16	15–17	14–17	16–17	14–16	14–16	15–16	14–16	13–14	16	14–15	16	17	14–15	15–16	15	16
Hypobranchial muscles	12	12	12–15	12–15	12	12–13	11–12	12	13	12	13	13	13	13	12–13	13	13	13
Pectoral muscles	17	15–16	16	16	17	15	16	16	17	16	17	17	17	14	15	14	14	14
Arm muscles	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	4
Forearm muscles	19	19	18	18	19	19	19	19	19	19	19	19	19	19	19	18	18	19
Hand muscles	30	30	30	34	32–36	22	22	22	21	27	27	27	27	27	27	20	20	26
Total number of muscles	130–132	127–130	128–135	133–139	133–138	117–120	118–121	118–119	119–121	123–126	129–131	128–130	131	129	117–119	119–120	126	123

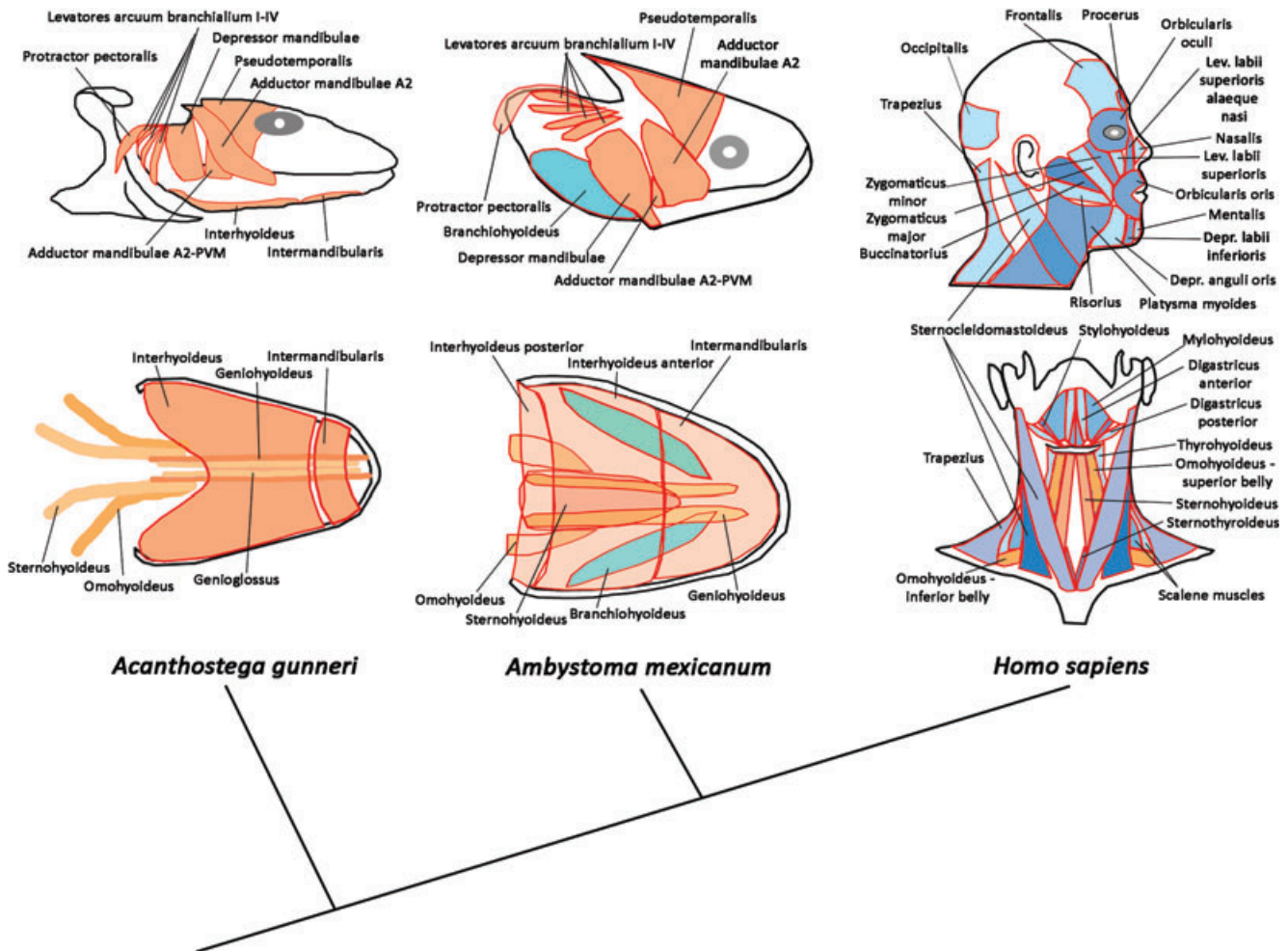


Fig. 1. Scheme showing the most superficial head and neck muscles in *Homo sapiens*, *Ambystoma mexicanum* and *Acanthostega gunneri* [based on our knowledge of the muscles present in the last common ancestor (LCA) of tetrapods: see Table 2 and text], to illustrate our notion of ‘anatomically plesiomorphic’ versus ‘derived’ taxa within a certain clade (top, right lateral views; bottom, ventral views with anterior part of heads to the left, except in the case of humans, where it is to the top). As can be seen, *Ambystoma mexicanum* is an anatomically plesiomorphic tetrapod in the sense that it is a very good model to study the origin and early evolution of the tetrapod muscles, keeping almost all the muscles that were present in the LCA of tetrapods (ancestral muscles shown in orange and red) and having very few new muscles that were not present in that LCA (new muscles shown in blue) (see Table 2). By contrast, *Homo sapiens* is an anatomically derived tetrapod in the sense that it displays almost no muscles that were present in the LCA of tetrapods and having numerous new muscles that were not present in that LCA (see Table 2).

species from each of the other major extant tetrapod clades, to Tables 1 and 2, in order to analyse and compare the variation of the percentages given within each of these clades.

As would be expected, the lizard *Timon lepidus* (Reptilia: Lepidosauria) is a less good model for the LCAT than axolots: only 76% (28) of its 37 pectoral and forelimb m/mg were present in the LCAT, keeping 28 (72%) of the ancestral 39 m/mg. However, it is a very good model for the LCA of amniotes (LCAA): 97% (36) of its 37 m/mg were present in the LCAA, keeping 36 (86%) of the 42 m/mg of the LCAA. As also would be expected, the platypus *Ornithorhynchus anatinus* (Mammalia: Monotremata) is a worse model for

both the LCAT and LCAA, but interestingly, is a good model for the pectoral and forelimb muscles of the LCA of mammals (LCAM): 100% (45) of its 45 m/mg were present in the LCAM, keeping 45 (90%) of the 50 m/mg of the LCAM. This contrasts with the idea, commonly defended in the literature, that monotremes are a good example of a ‘phylogenetically basal taxon’ within a clade (mammals) that includes species displaying, in general, a highly derived, peculiar (and *not* a plesiomorphic) musculoskeletal anatomy for that clade (e.g. Jouffroy & Lessertisseur, 1971).

Lastly, *Lemur catta* (Primates: Strepsirrhines) appears as a remarkably good model for the LCA of primates (LCAP): 100% (55) of its 55 m/mg were present in

the LCAP, keeping all (100%) of the 55 muscles of the LCAP (Table 1). Modern humans, *Homo sapiens*, appear to be a worse model for any of the LCAs shown in Table 1: of their 50 pectoral and forelimb m/mg, only 21 (42%) were present in the LCAT, 27 (54%) in the LCAA, 37 (74%) in the LCAM, and 45 (90%) in the LCAP, keeping only 54% (21/39), 64% (27/42), 74% (37/50) and 82% (45/55) of the m/mg of those LCAs, respectively. In summary, the data provided in Table 1 strongly support the idea that, at least concerning their pectoral and forelimb muscles, taxa such as salamanders, lizards, monotremes and lemurs do provide good models to study and discuss the origin and early evolution of, respectively, tetrapods, amniotes, mammals and primates.

Table 2 shows the same taxa and type of calculations shown in Table 1, but for the head and neck muscles. Concerning the identity and number of these muscles, axolotls, as well as frogs such as *Rana pipiens*, are good models for the LCAT: they both have 17 (94%) of the ancestral 18 m/mg (the pterygomandibularis, present in amniotes and some amphibians, e.g. caecilians, is absent in both of these taxa). Eighty five and 89% of the structures found in axolotls and *Rana pipiens* were present in the LCAT, the two taxa having respectively only three and two muscles that were lacking in that LCA (branchiohyoideus, interradians and laryngeus, in axolotls; interscapularis and adductor mandibulae A2 lateralis, in *Rana pipiens*). Lizards such as *Timon lepidus* also have 17 (94%) of the m/mg found in the LCAT, but have many more new m/mg (eight in total), and therefore only 68% of their structures were present in that LCA. Lizards are, however, a better model for the LCAA, because 20 (80%) of the 25 m/mg of *Timon lepidus* were present in the LCAA, keeping all the 20 (100%) m/mg of the LCAA. As would be expected, monotremes appear to be a much worse model for the LCAT and LCAA, but surprisingly they are, again, a very good model for the LCAM (see also Table 1): of the 31 m/mg of platypus 30 (97%) were present in the LCAM, keeping 30 (94%) of the 32 m/mg of the LCAM. Lastly, lemurs and modern humans are poor models for the LCAT (see Fig. 1), LCAA and LCAM. Lemurs are a very good model for the LCAP, keeping 35 (90%) of the 39 m/mg of the LCAP and not having any new muscles absent in the LCAP. Modern humans appear as a surprisingly good model of the LCAP, keeping 36 (92%) of the 39 m/mg of that LCA, which account for 92% of the 39 human m/mg shown in Table 2. The numbers and percentages given in Table 2, as well as in Table 1, will be discussed further in Section III.

We stress that we are obviously not the first authors to defend that taxa such as urodeles (and particularly non-neotenic salamanders: see above) and lemurs are particularly good models to study the origin and early evolution of tetrapods and of primates, respectively. Examples of researchers that have used salamanders

to study the ancestral Bauplan of tetrapods include Humphry (1872*a,b*), Gregory (1929), Howell (1935, 1936*a,b*, 1937*a,b*), Straus (1941*a,b*) and Goodrich (1930), and, more recently, Clack (2002), Shubin (2008) and Kawano *et al.* (2013). As explained in Section I, most discussions on the evolution of vertebrates made by other authors have been based on hard tissues; therefore, most of the studies that have used urodeles to infer aspects of the ancestral tetrapod Bauplan have been based mainly on skeletal features. However, some of those studies did include information about soft tissues, particularly during the last decades of the 19th Century and the first half of the 20th Century (e.g. Humphry, 1872*a,b*; Howell, 1935, 1936*a,b*, 1937*a,b*; Straus, 1941*a,b*), the golden age for vertebrate comparative myology (Diogo & Abdala, 2010). However, the discussions provided in those studies about the origin and evolutionary history of tetrapod musculature were often based on qualitative superficial comparisons of muscles that did not include explicit phylogenetic or quantitative analyses, such as the phylogenetic analyses provided for example by Diogo & Wood (2011, 2012*a*), from which the quantitative data presented in Table 3 were obtained. Furthermore, these myological studies did not address broader topics such as the notions of *scala naturae*, 'progress' or increased complexity in biological evolution. More recent works on tetrapod early evolution have in general neglected information about muscles (e.g. Clack, 2002; Hall, 2007; Shubin, 2008). For example, in a recent excellent book dedicated to discussing the evolutionary, phylogenetic and developmental contexts of the transformations from fins to limbs edited by Hall (2007), there is no mention of muscles.

However, it also needs to be emphasized that some authors, particularly in the last decades, have stated that salamanders are not a good model to study the origin and early evolution of the tetrapod Bauplan (e.g. Wagner *et al.*, 1999; Stopper & Wagner, 2007). Some of the reasons given by these authors are based on empirical data, while some others are mainly theoretical, reflecting the changes of ideas that have occurred within the field of evolutionary biology during these last decades, as explained in Section I. Concerns about urodeles as an 'anatomically plesiomorphic' tetrapod model are, for instance, based on the ontogeny of their limbs. For example, while digit formation in urodeles usually occurs from the most radial/tibial digit (digit 1) to the most ulnar/fibular digit (digit 4 in the hand, 5 in the foot), in anurans, as well as in most amniotes studied so far, the last digits to form are usually the most radial/tibial digits (e.g., Alberch & Gale, 1983; Gilbert, 2006; Fröbisch & Shubin, 2011). The existence of different morphogenetic gradients (e.g. radio/tibio-ulnar/fibular *versus* ulno/fibulo-radial/tibial) of skeletal limb patterning in tetrapods shows a remarkable plasticity

regarding limb morphogenesis and makes it difficult to discern the ancestral tetrapod state. In this particular respect, authors have argued that because the ulno/fibulo–radial/tibial skeletal morphogenetic gradient is usually found in both frogs and amniotes, the phylogenetically most parsimonious hypothesis is that such a gradient represents the ancestral condition for tetrapods (see Fröbisch & Shubin, 2011, for a review). But such hypotheses about the origin and early evolution of the tetrapod Bauplan rely almost exclusively on studies of hard tissues and, in this specific case, of limb skeletal patterning.

In fact, in contrast to those studies, our recent ontogenetic and regenerative studies of the limb muscles of salamanders and frogs strongly support the idea that salamanders are actually a very good model to discuss the origin and development of the ancestral tetrapod limb Bauplan (e.g. Diogo & Tanaka, 2012, 2014; Diogo & Ziermann, 2014; Diogo, Nacu & Tanaka, in press; Diogo, Murawala & Tanaka, 2014). For instance, it is now clear that the pelvic/thigh muscles of the first tetrapods were very different topologically to the pectoral/arm muscles, as the pectoral and pelvic girdle muscles have been in the vast majority of fish, supporting the idea that the pelvic and pectoral appendages of vertebrates are not serial homologues (Diogo *et al.*, 2013*a*). By contrast, the forearm/hand and leg/foot muscles of the first tetrapods were very similar probably due to a derived cooption, during the fin–limb transition, of some similar genes for the development of the zeugopodia and autopodia, which are mainly *de novo* structures (Diogo *et al.*, 2013*a*). In salamanders, all the leg/foot and forearm/hand muscles have a clear ‘topological equivalent’ in the other limb, with the exception of the flexor antibrachii et carpi radialis and flexor antibrachii et carpi ulnaris (Diogo, 2014). However, there is some evidence indicating that in the first tetrapods the musculature of the leg–foot was probably even more strikingly similar to the musculature of the forearm–hand than is the case in these anatomically plesiomorphic extant tetrapods. For example, the comparative studies of McMurrich (1905) and Bardeen (1906) suggested that, in extant salamanders, the distal (leg) portion of the ischioflexorius corresponds to an ancestral muscle flexor cruris et tarsi tibialis, while the femoral head of the flexor digitorum communis corresponds to an ancestral muscle flexor cruris et tarsi fibularis.

Our recent ontogenetic studies of the axolotl limb muscles reinforced the idea that the distal (leg) portion of the ischioflexorius corresponds to an ancestral muscle flexor cruris et tarsi tibialis and indicate that the femorofibularis (and not the flexor digitorum communis) might correspond to an ancestral muscle flexor cruris et tarsi fibularis (Diogo & Tanaka, 2014). It seems clear that if a flexor cruris et tarsi fibularis is represented by either the femorofibularis and/or by

part of the flexor digitorum communis, the ancestral Bauplan of the zeugopodial and autopodial musculature of both limbs is even more strikingly similar than is usually assumed. This similarity is less apparent in adult salamanders, because in the forearm the muscle/muscles derived from each anlage are present as distinct muscles, while in the leg the flexor cruris et tarsi tibialis is fused with the thigh portion of the muscle ischioflexorius, and the flexor cruris et tarsi fibularis either migrated slightly proximally (forming the femorofibularis) and/or became fused with the flexor digitorum communis (Diogo & Tanaka, 2014). Therefore, it is very likely that in the first tetrapods all the forearm/hand muscles had a topological ‘equivalent’ in the hindlimb and this striking similarity is still seen, to a lesser degree, in urodeles because these amphibians have flexor antibrachii et carpi radialis/ulnaris anlagen and also seem to have flexor cruris et tarsi tibialis/fibularis anlagen. Importantly, our recent developmental studies of axolotls also indicate that, in the first tetrapods, the dorsal forearm musculature was not only strikingly similar to the dorsal leg musculature but also to both the ventral forearm and leg musculature (dorso-ventral symmetry). This is because the forelimb and hindlimb also have extensor antibrachii et carpi radialis/ulnaris and extensor cruris et tarsi tibialis/fibularis anlagen, respectively (Diogo & Tanaka, 2014). That is, the first tetrapods probably had a very similar configuration in the eight sides of the four zeugopodia (i.e. dorsal and ventral sides of the four limbs), with a recognizable central muscle [extensor digitorum (longus)/flexor digitorum communis] surrounded by radial/tibial and ulnar/fibular muscles (derived by the flexor/extensor antibrachii/cruris et carpi/tarsi radialis/tibialis/ulnaris/fibularis anlagen). This stresses, once again, how axolotls and other urodeles are particularly good models to study and discuss the origin and early evolution of tetrapods.

In this context, the results of our recent developmental and regenerative studies of limb development thus make us more careful about the idea, mentioned above, that for instance regarding the morphogenetic gradients of limb patterning salamanders are not good models to infer the ancestral tetrapod limb Bauplan. By providing the first detailed ontogenetic and regenerative studies of all axolotl limb muscles and developmental studies of the limb musculature of some frogs, we have shown that almost all autopodial muscles of both limbs develop following the same skeletal morphogenetic gradient found in each of these taxa (i.e. radio/tibio–ulnar/fibular in axolotls *versus* ulno/fibulo–radial/tibial in frogs) (Diogo & Tanaka, 2012, 2014; Diogo & Ziermann, 2014; Diogo *et al.*, 2014). These new data therefore complement the data that have been obtained previously in the skeletal developmental works cited above about the skeletal morphogenetic gradients of anurans and amphibians (Alberch

& Gale, 1983; Gilbert, 2006; Fröbisch & Shubin, 2011), allowing researchers to have a wider, more integrative view of the relationships between hard and soft tissue formation. By showing that the morphogenetic gradients of muscle formation and differentiation in the autopodia are similar to the skeletal morphogenetic gradients of bone formation, these new data do not support or contradict, by themselves, the hypothesis that the ulno/fibulo–radial/tibial gradient usually seen in frogs and amniotes might be ancestral for tetrapods. But, on the other hand, by combining these data with the other new myological data obtained by us indicating that when one studies the ontogeny of urodeles it becomes even more clear that these animals are a good model for studying the ancestral tetrapod Bauplan than previously expected (see above), one is stimulated to be more careful about accepting this hypothesis too easily. That is, one should at least consider the possibility that the occurrence of radio–ulnar/tibio–fibular, as well as of proximo–distal, gradients seen in both the regeneration and ontogeny of both limbs in axolotls might represent the ancestral condition for tetrapods. Such a condition could for instance be explained by a dependence of muscle patterning upon the patterning of connective tissue. This is because both in axolotl development and regeneration, as well as in the ontogeny of other tetrapods in general, there are many markers and patterning genes that have been extensively implicated in patterning of limb connective tissue and that are upregulated in proximo–distal (e.g. *Hox*, *FGFs*, *RA*) and radio–ulnar and/or tibio–fibular fashion (e.g. *Shh*) (e.g. Gilbert, 2006; Carlson, 2007). It is therefore possible that either these molecules have direct impact on muscle patterning or that they can influence muscle patterning *via* patterning of connective tissue. But the hypothesis that a radio–ulnar/tibio–fibular gradient might be ancestral for tetrapods should obviously be tested in face of all the data available, and for that purpose more developmental mechanistic studies, and particularly more palaeontological studies ideally including information about limb ontogeny in early tetrapod and amphibian fossils, needs to be obtained and then discussed in a broader context.

III. SCALA NATURAE, PROGRESS, REVERSIONS AND HUMAN EVOLUTION

As explained in Section I, the idea of *scala naturae* dates back to thinkers such as Aristotle; the basis of the idea that there is a ‘progression’ from ‘lower’ plants and worms to ‘higher’ human beings was, therefore, not evolutionary, but reflected the degree of difference between other organisms and ourselves (Bonner, 1988). As noted by Bonner (1988), in an early notebook Darwin cautioned that we should never use the terms ‘lower’ and ‘higher’ taxa, but he did not follow his own advice

in his later publications (see also, e.g. Richards, 1992). Nowadays, few researchers would explicitly defend the notion of progress underlying the *scala naturae* but, as with Darwin, numerous authors continue to use the terms ‘lower’ and ‘higher’ taxa, renewing interest in the issue (e.g. Moore, 2013; Rigato & Minelli, 2013). As explained in Section I, in *The evolution of complexity* Bonner (1988) stated that modern humans are, phenotypically, the most complex organisms on the planet, although he did not provide any empirical data to support this statement. As shown in Table 3, and as will be discussed further below, the results of our empirical research on the comparative anatomy of modern humans and other mammals clearly contradict Bonner’s (1988) statement in the sense that, at least in terms of number of striated muscles, modern humans are clearly less complex (more simplified, i.e. with fewer muscles) than both many non-human primate and non-primate mammals. Within the context of the present paper and of our myological comparisons of the taxa listed in Table 3, the most appropriate, simple, succinct and objective way to measure complexity is to compare the number of skeletal muscles of each taxon, because each muscle is the result of parcellation, i.e. of innovation through differentiation leading to a morphogenetic semi-independence of the muscle (*sensu* Vermeij, 1973). This is because: (i) the number of muscles is a objective measure (e.g. the numerous researchers studying, and anatomical atlases focussed on, human gross anatomy agree in their recognition of which skeletal myological structures are muscles and therefore describe the same number of muscles in the human body); (ii) by using this way of measuring complexity, we combine a macroevolutionary definition of complexity similar to that of Bonner (1988); the only difference being that Bonner referred to the number of different types of cells instead of the number of muscles) with a developmental definition of complexity that includes the notions of parcellation (e.g. Wagner & Altenberg, 1996) and of morphogenetic semi-independence (e.g. Vermeij, 1973). It should be stressed that there are obviously many possible ways to define complexity in biology, and that for the specific purpose of the present paper we are using a morphological definition of complexity (see reviews of Eble, 2004, 2005, for more details on this subject).

Moreover, Bonner (1988) also illustrates the confusion that researchers often exhibit between the original idea of *scala naturae* and the use of the terms ‘lower’ and ‘higher’ taxa. On the one hand he recognized that this idea is related to the notion of a progression in complexity from ‘lower’ organisms such as bacteria to the ‘highest’ of all animals, humans. But, on the other hand, he then states ‘paleontologists [...] refer to strata as upper and lower, for they are literally above and below each other [...]; these fossil organisms in the lower strata will, in general, be more primitive in structure as well as belong to a fauna and flora of earlier

times, so in this sense “lower” and “higher” (taxa) are quite acceptable terms’ (Bonner, 1988, p. 6). There are two main problems with this latter statement. Firstly, there are many examples of how older animals (from ‘lower’ strata) are often considered, in various aspects of their biology and physiology, more complex than more recent ‘higher’ animals (from ‘higher’ strata). For instance, many researchers would argue that, in many aspects of their anatomy and physiology, taxa such as rats are not necessarily more complex than taxa such as dinosaurs or plesiosaurs (e.g. Gould, 2002). Secondly, and perhaps more important in the context of the present review, in the original idea of *scala naturae* the term ‘higher’ taxa referred to humans and to the animals that are anatomically more similar to humans, and this is still the way in which this term is used by many authors nowadays (reviewed by Diogo & Wood, 2012a, 2013). That is, amniotes are seen as ‘higher’ than amphibians, mammals as ‘higher’ than reptiles, primates as ‘higher’ than other mammals, hominoids as ‘higher’ than other primates, and humans as ‘higher’ than other hominoids. This is precisely the reason why non-monophyletic groups such as apes, which refers to non-human hominoids, are still much in use at present. So, when Bonner (1988) refers to ‘higher’ taxa as the taxa that are found in higher (more recent) strata, he is confusing the original idea of *scala naturae*. For instance, modern humans (*Homo sapiens*) originated more than 200000 years ago, while many new species of cichlid fish originated in the last 15000 years; however, under the original *scala naturae* idea this would never mean that these cichlid species are ‘higher’ than *Homo sapiens*, or for instance, than primate taxa such as some extinct species of New World Monkeys that lived about 40 million years ago (for a review of the approximate times of origin of all these taxa, see e.g. Dawkins, 2004).

The last point precisely illustrates the major problem of using the terms ‘higher’ and ‘lower’ taxa: they are deeply and directly related to the idea that humans and their closest relatives are the goal of a progression towards a higher level of complexity, or at least to the fact that humans operate in an anthropocentric framework that colours their research questions and data interpretations. So, the term ‘lower’ taxon, for instance, does not correspond at all to the terms ‘phylogenetically basal’ and/or ‘anatomically plesiomorphic’ taxon as used in the present review. For instance, in the *scala naturae* idea of progression towards humans, a primate such as a lemur would be considered ‘higher’ than an elephant, but in many aspects of their anatomy and physiology (e.g. the remarkable differentiation of the facial muscles of elephants and the configuration and movements of their proboscis) elephants are more anatomically more complex than lemurs. To give a clear, objective example supporting this latter statement, and following the examples provided in Section II, it can be said that, for instance, elephants kept less facial muscles

that were present in the LCA of placentals, and acquired many more new facial muscles that were not present in that LCA, than did lemurs (Boas & Paulli, 1908; Diogo & Abdala, 2010; Diogo & Wood, 2012a). This is why we consider that the terms ‘higher’ and ‘lower’ taxa should be avoided, while the term ‘anatomically plesiomorphic’ should be retained, as long as it is used to refer to specific taxa within the context of a particular set of characters/body region and of a specific clade. So, for instance, one can say that regarding the number and identity of the facial muscles, elephants are anatomically derived placental mammals, and regarding the number and identity of their pectoral and forelimb muscles lemurs are anatomically plesiomorphic primates (Table 1; Section II). As explained in Section I, Bonner himself has changed many of the ideas expressed in his earlier book (Bonner, 1988), and recently published a small, elegant book *Randomness in evolution* (Bonner, 2013) in which he explains his current interpretations, which are in general more close to the views defended in the present review.

The use of the terms ‘phylogenetically basal/derived’ taxa is, in our opinion, more delicate and controversial. Some authors could argue that, for instance, to say that the Strepsirrhini is a phylogenetically basal clade within the order Primates would be anthropocentric. This is because this clade is the sister-group to the Haplorhini clade (tarsiers + anthropoids), and would be considered to be ‘basal’ just because humans happen to be haplorhines. However, given the now consensually accepted view that there are five major groups of extant primates (i.e. strepsirrhines, tarsiers, New World monkeys, Old World monkeys and hominoids), strepsirrhines are effectively the sister-group of the clade that includes all the other four major extant primate groups. Note that it could be argued that the recognition of the four major non-strepsirrhine primate groups is itself due to anthropocentrism, i.e. to our tendency to recognize more groups in the clade that includes humans. Contrarily, it was precisely the persistence of the *scala naturae* idea that led to the previous non-recognition of one of these four haplorhine groups as a consequence of an erroneous grouping of the strepsirrhines and tarsiers in a ‘Prosimii’ clade, which was considered to be the sister-group of the ‘higher’ primates, the anthropoids. Moreover, in general the anatomy of strepsirrhines (particularly taxa such as lemurs) is more similar to that of the LCAP of than is that of tarsiers, New World monkeys, Old World monkeys and hominoids (see Section II; Tables 1 and 2; for more details, see Diogo & Wood, 2011, 2012a, 2013), and the members of these four latter groups have effectively accumulated more phylogenetic anatomical character-state changes since the LCAP than did the strepsirrhines (as we will show below). Also, importantly, the number of extant strepsirrhine species is much smaller than the number of all other extant primate species (reviewed by Diogo &

Wood, 2012a). It therefore makes sense, in our opinion, to state that strepsirrhines are the phylogenetically most basal extant primates, because they are the sister-group of the clade that includes all the other, phylogenetically more derived (e.g. in terms of number of accumulated phylogenetic character-state changes) and taxonomically diverse (in terms of number of species) extant primate taxa. One of the criticisms of the tree-thinking advocates is that this type of reasoning can be flawed, because groups that are taxonomically less diverse nowadays could have been more diverse at some other geological period (e.g. Gregory, 2008; Casane & Laurenti, 2013). However, in this specific case concerning the clade Strepsirrhini, even if we include all known primate extinct taxa in the comparisons it is clear that this clade includes by far fewer species than the Haplorhini clade (reviewed by Diogo & Wood, 2012a).

Perhaps a better way to show how using the terms phylogenetically basal/derived taxa is not necessarily anthropocentric or influenced by the notion of *scala naturae* is the fact that these terms are often also used to refer to taxa from clades that do not include humans. For instance, the Amphicoela clade including *Ascaphus* and *Leiopelma* is often considered to be the most phylogenetically basal clade of extant anurans, because it is the sister-group of the clade including all other extant anurans (e.g. Irisarri *et al.*, 2011). It would be very difficult to argue that only humans would see this clade as the most phylogenetically basal within extant anurans, instead of the clade including all the other, numerous living anuran genera. This also provides a good example of how being too politically correct could be counter-productive and even go against basic common sense. For instance, designating the Amphicoela clade as phylogenetically basal within extant anurans clearly helps communication between phylogeneticists, evolutionary biologists, and developmental biologists; by using such a designation, biologists do not have to check and know all the details of the whole anuran phylogenetic tree in order to understand that the Amphicoela clade is the sister-group of a clade that includes all the other extant amphibians. Also, and importantly in the context of the present review, this is an example in which using the term 'phylogenetically basal' for the Amphicoela anuran clade allows other researchers to make biological predictions and focus their biological questions; in this case, as in many others, the clade includes the two genera that are, in many aspects, the anatomically most plesiomorphic extant anurans. For instance, in terms of the number, identity and overall configuration of their pelvic and hindlimb muscles, *Ascaphus* and *Leiopelma* are more similar to the LCA of anurans than are any other extant anuran taxa (e.g. Dunlap, 1960).

In the remaining paragraphs, we stress the differences between the idea of *scala naturae* and the associated notion of evolutionary progression from 'lower' to more complex, 'higher' organisms, and the use of

the terms 'anatomically plesiomorphic' and 'phylogenetically basal' taxa in the sense they are used by us. For this purpose, we use the empirical data obtained in our comparative and phylogenetic studies of primate musculature (Diogo & Wood, 2011, 2012a,b), because they allow us to compare directly the number of muscles found in various primate taxa (Table 3) and the number of phylogenetic (evolutionary) steps that have led to the myological configuration found in those taxa. First we provide a short summary of the relevant data that allow discussion, from a new angle, of the specific issues treated herein.

Firstly, we emphasize that a phylogenetically basal taxon within a certain clade (*sensu* the present review) does not necessarily include anatomically plesiomorphic taxa that can be used as good models for the LCA of all extant taxa of that clade. For instance, the infraorder Tarsiiformes is phylogenetically basal within the clade Haplorhini because it includes only three extant genera and is the sister-group to the infraorder Simiiformes (Anthropoidea) that includes all other, numerous haplorhine species of New World monkeys, Old World monkeys and hominoids (apes and humans). However, as shown in Table 3 and explained in detail by Diogo & Wood (2011, 2012a, 2013), tarsiers display a highly peculiar mix of muscles that were present in the LCA of haplorhines and numerous new, unique muscles that were not present in that LCA, thus having in total more head, neck, pectoral and forelimb muscles than any other extant primate. Thus, regarding muscle anatomy, tarsiers do not provide a good model for the LCA of haplorhines and thus to discuss the origin and early evolution of these muscles in the Haplorhini.

Secondly, it is interesting and somewhat ironic to note that in some aspects the numbers provided in Tables 1 and 2 seem to provide some support for the idea of *scala naturae*, and that it is the evolution of our own species and of our own order, the primates, that constitutes the main problem for this anthropocentric idea. For instance, amphibians such as axolotls have fewer pectoral and forelimb (PF) as well as head and neck (HN) m/mg (33 PF, 20 HN) than reptiles such as lizards (37 PF, 25 HN) which have fewer than mammals such as monotremes (45 PF, 31 HN), which in turn have fewer than primates such as lemurs (55 PF, 35 HN). But modern humans have fewer pectoral and forelimb m/mg (50 PF) than lemurs (Table 1). Modern humans do have more head and neck m/mg than lemurs (39 HN; Tables 2 and 3), but even if we count every muscle and include both cranial and postcranial muscles, modern humans still have fewer muscles than lemurs and many other primates (Table 3).

At first sight, the numbers provided in these comparisons could seem paradoxical because our cladistic analyses suggest there are more unambiguous evolutionary steps from the base of the primate tree to modern humans than to any other primate taxon included in

Table 3 (Diogo & Wood, 2011, 2012*a*). For instance, the results of our primate parsimony and Bayesian analyses based on muscles indicate that, at least regarding the gross morphology of the head and neck musculature, since the *Pan/Homo* split, the clade Hominina has evolved faster than the panin clade (about 2.3 times faster according to the lengths of the branches leading to modern humans and to chimpanzees in our parsimony tree; Diogo, Peng & Wood, 2013*b*). However, humans have fewer muscles than chimpanzees and even than primates such as tarsiers or the anatomically plesiomorphic lemurs (see above; Table 3). As pointed out by Gould (2002), there is a general tendency to use ‘progressive trends’ to tell evolutionary stories, particularly in palaeontological publications, in which examples of stasis are often either unreported or under-reported because stasis is interpreted as ‘no data’. The results of our study support Gould’s (2002) contention in the sense that, contrary to the original *scala naturae* idea and the associated notion of progression towards greater complexity, there is effectively no general trend to increase the number of muscles at the nodes leading to hominoids and to modern humans. That is, with respect to the muscles in the regions we have investigated, although modern humans accumulated more evolutionary transitions than the other primates included in our cladistic study, these evolutionary transitions did not result in more muscles, or more muscle components (Diogo & Wood, 2011, 2012*a,b*; Diogo *et al.*, 2013*b*). For instance, although some of the nine modern human apomorphies acquired since the *Pan/Homo* split involve the differentiation of new muscles (e.g. rhomboideus major and rhomboideus minor, extensor pollicis brevis and flexor pollicis longus), others involve the loss of muscles (e.g. levator claviculae and dorsoepitrochlearis). As a result, more muscle changes were accumulated in our evolutionary history than in that of modern chimpanzees, but modern chimpanzees present more head and neck and pectoral and upper limb muscles than *Homo sapiens* (Table 3). In fact, with respect to the number of head, neck, pectoral and forelimb muscles, one could make the case that modern humans are relatively simplified primates (Table 3; Diogo & Abdala, 2010).

The empirical data obtained in our comparative and phylogenetic studies of primate musculature also contradict the notion of an evolutionary progressive trend because these data clearly stress the importance of homoplasy and of evolutionary reversions in primate morphological evolution. As noted in Diogo & Wood (2012*b*, 2013), reversions played a substantial role in primate and human evolution because 1 in 7 of the 220 evolutionary transitions unambiguously optimized in their most parsimonious primate phylogenetic tree (concerning changes in the head, neck, pectoral and forelimb musculature) are reversions to a plesiomorphic state. Importantly, of those 28 reversions, six played a direct

role in our own evolution for they occurred at the nodes that led to the origin of modern humans. Moreover, 9 of those 28 reversions violate Dollo’s law, which states that when complex structures are lost in evolution, they cannot be reacquired (Diogo & Wood, 2012*b*). The important role played by evolutionary reversions in the evolution of our own clade, as well as of many other animal clades (see, e.g. Wiens, 2011), and the fact that many of these reversions do violate Dollo’s law clearly goes against the *scala naturae* idea that there is a lineal progression in evolution towards ‘higher’, more complex animals.

IV. CONCLUSIONS

(1) The inclusion of soft-tissue-based information in evolutionary and phylogenetic investigations allows us to undertake a fresh, original discussion of broader evolutionary issues such as those concerning the *scala naturae*, i.e. the notion of lineal progression in evolution. Here we contradict this notion of *scala naturae*, and the use of the terms ‘lower’/‘higher’ associated with it, but stress that the refutation of this old notion does not mean that one should avoid using terms such as phylogenetically basal and, especially, ‘anatomically plesiomorphic’ taxa.

(2) With respect to the number, identity and configuration of their pectoral, forelimb, head and neck muscles, urodeles (and particularly non-neotenic salamanders), lizards and lemurs can be regarded as good models to study the origin and early evolution of tetrapods, amniotes and primates, respectively; notably, the monotreme platypus appears a surprisingly good model to study the origin and early evolution of both cranial and postcranial muscles in mammals.

(3) It is particularly interesting, and somewhat ironic, to see that, regarding the number of muscles, the evolution of our own species and of our own order, Primates, actually constitutes a problem for the anthropocentric idea of a *scala naturae* within the data shown in Tables 1–3. In fact, concerning the number of head, neck, pectoral and forelimb muscles, although modern humans accumulated more evolutionary transitions than the other primates studied by us, these evolutionary transitions did not result in more muscles. These transitions actually involved the complete loss of some muscles, resulting in the fact that, with respect to the number of myological structures, modern humans are actually relatively simplified primates.

(4) This review will hopefully contribute to the knowledge of anatomical evolution and to future evolutionary, phylogenetic and developmental studies, by showing how salamanders provide a particularly good evolutionary and developmental model to study the origin and early evolution of tetrapods. For instance, developmental biologists tend to view the pattern

of digit formation in salamanders (radial/tibial to ulnar/fibular) as a derived feature within tetrapods because in frogs and amniotes the radial/tibial digits are usually the last to form. However, our recent developmental and regenerative studies of salamanders, frogs and other amniotes have strongly reinforced the idea that urodeles are, in general, an especially good model to study the origin and development of the ancestral tetrapod limb Bauplan. Therefore, it would be interesting to combine data obtained from developmental, regenerative and comparative morphological studies, not only on hard, but also on soft tissues, with palaeontological data in order to reach a more integrated and comprehensive understanding of which anatomical and ontogenetic features are, or are not, part of that Bauplan. In fact, because we lack definitive modern analogues of transitional forms (reviewed in Pierce, Hutchinson & Clack, 2013), the best means to understanding the stepwise changes in functional morphology that accompanied the transition from aquatic to terrestrial tetrapod locomotion is rigorous analysis of fossil material combined with comparative anatomical studies of their extant relatives. As recently stressed by Pierce *et al.* (2013), previous studies have mainly focussed on changes in the limb skeleton; very few have attempted to reconstruct the muscular anatomy of early tetrapods. Therefore more studies including myological data are needed to understand better the fascinating anatomical and functional changes that occurred during the transitions from fish to tetrapods and that allowed the latter to explore an impressively wide range of habitats.

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(Received 28 August 2013; revised 28 April 2014; accepted 13 May 2014)