

The broader evolutionary lessons to be learned from a comparative and phylogenetic analysis of primate muscle morphology

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ABSTRACT

The present publication reviews the broader evolutionary implications of our long-term study of primate musculature. It summarizes the implications of the study for our understanding of the use of myological characters for phylogenetic reconstruction, for assessing the importance of homoplasy and reversions in evolution, and for our understanding of Dollo's law, the notion of 'direction' in evolution, the common myth of human complexity, the tempo and mode of primate and human evolutionary history, adaptive radiations, the notion that 'common' equals 'primitive' and the influence of morphogenesis on the variability of head, neck, pectoral and upper limb muscles. Among other results our study shows that myological characters are useful for phylogenetic reconstruction. The results also stress the importance of homoplasy and of evolutionary reversions in morphological evolution, and they provide examples of reversions that violate Dollo's law due to the retention of ancestral developmental pathways. They also show that contrary to the idea of a 'general molecular slow-down of hominoids' the rates of muscle evolution at the nodes leading to and within the hominoid clade are higher than those in most other primate clades. However, there is no evidence of a general trend or 'directionality' towards an increasing complexity during the evolutionary history of hominoids and of modern humans in particular, at least regarding the number of muscles or of muscle bundles. The rates of muscle evolution at the major euarchontan and primate nodes are different, but within each major primate clade (Strepsirrhini, Platyrrhini, Cercopithecidae and Hominoidea) the rates at the various nodes, and particularly at the nodes leading to the higher groups (i.e. those including more than one genus) are strikingly similar. Our results also support, in general terms, the assumption that 'common is primitive' and they lend some support for the 'vertebrate-specific model' in the sense that during the divergent events that resulted in these four major primate clades there was more emphasis on postcranial changes than on cranial changes. Our study of primates does not, however, support suggestions that the distal structures of the upper limb are more prone to variation than the proximal ones, or that the topological origins of the upper limb muscles are more prone to evolutionary change than their insertions.

Key words: evolution, development, morphogenesis, muscles, homoplasy, phylogeny, primates, rates, reversions.

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I. INTRODUCTION

Most studies of the gross morphology of the soft tissues of primates (reviewed in Gibbs, Collard & Wood, 2002) are either in-depth investigations of a single structure or organ, or investigations that focus on a single taxon. The reasons for these choices are that the type of detailed morphological familiarity needed for this type of research takes many years to acquire, specimens of primates are difficult to come by, and the investigations are time-consuming. We resolved to overcome these difficulties and began by undertaking a detailed study of the head, neck, pectoral and upper limb myology of each of the major primate higher taxa plus a range of outgroups, including rodents (Rodentia: e.g. *Rattus*) and the two extant groups that are more closely related to primates, i.e. the tree-shrews (Scandentia: e.g. *Tupaia*) and ‘flying lemurs’ (Dermoptera: e.g. *Cynocephalus*) (see Figs 1–3). We have now embarked on a second study that focuses on the muscles of the trunk, pelvic and lower limb. Our study of primates is part of a long-term project to investigate the comparative anatomy, homologies and evolution of the striated muscles of all of the major groups of vertebrates (Diogo, 2007; Diogo & Abdala, 2007, 2010; Diogo *et al.*, 2008, 2009*a,b*; Abdala & Diogo, 2010). We have also published anatomical atlases of non-human higher primate taxa (e.g. Diogo *et al.*, 2010, 2012*a*, 2013, in press-*b*) that include descriptions and photographs of all of the muscles, and papers that report the results of comprehensive parsimony and Bayesian cladistic analyses of the myology of these taxa (e.g. Diogo & Wood, 2011, 2012*b*; Diogo, Richmond & Wood, 2012*b*; Diogo, Peng & Wood, ; in press-*a* see Figs. 1–3).

The title and content of this review was inspired by Wake’s recent review of what he learned from his own much longer term study of salamanders (Wake, 2009). Our goal is to draw together the broader evolutionary implications of our study of the head, neck, pectoral and upper limb musculature of primates. We consider the implications of that study for: (i) the use of myological characters in phylogenetic reconstruction; (ii) the importance of homoplasy and reversions; (iii) Dollo’s law; (iv) the directionality of evolution and the myth of human complexity; (v) the tempo and mode of primate and human evolutionary history; (vi) adaptive radiations and the notion of ‘common is primitive’; and (vii) the influence of morphogenesis on the variation among head, neck pectoral and upper limb muscles. Some of these topics have been addressed in our previous publications but the results have not previously been integrated; other topics are addressed here for the first time using previously unpublished analyses of our data. This synthesis will not only contribute to increasing the knowledge of morphological evolution in general, but

also serve to stimulate future analyses of the myology of other major mammalian and vertebrate groups.

II. THE USE OF MYOLOGICAL CHARACTERS FOR PHYLOGENETIC RECONSTRUCTION

Most phylogenetic studies of tetrapods and other vertebrates are based on hard tissue and/or molecular data. To address the paucity of myological phylogenetic studies, Diogo (2004*a,b*) compared the incidence of homoplasy and the utility of 91 myological and 303 osteological characters used in the reconstruction of the higher level phylogeny of a diverse group of teleosts, the Siluriformes (or catfish). Before discussing the results of the phylogenetic studies of Diogo and colleagues, it is appropriate to explain that the myological characters included in those works refer mainly to the presence/absence of muscles or muscle bundles and the attachments and innervation of these structures; features such as their internal architecture, type (e.g. slow *versus* fast), mass, or the direction of their fibres were not included. The results of Diogo (2004*a,b*) indicate that osteological structures generally display more morphological variation (i.e. incorporate more character states) than do myological ones. However, myology-based characters are generally more effective at recovering the relationships among higher clades that are supported by molecular data. Diogo (2007) increased the scope (a total of 356 characters in 80 extant and fossil terminal taxa) and reach of his cladistic analyses by extending them to include the whole osteichthyan clade (bony ‘fish’ plus tetrapods), and also found that hard tissue structures (bones and cartilages) displayed more variation than the myological ones. Whereas the 81 osteological structures examined for Diogo’s (2007) cladistic analysis provided 198 phylogenetic characters (i.e. 2.4 phylogenetic characters per osteological component), the 63 muscles examined provided 122 phylogenetic characters (i.e. 1.9 phylogenetic characters per muscle). However, the mean retention index (RI) of the informative muscular characters (0.82) was higher than that of the informative osteological characters examined (0.71) (i.e. the myological characters were on average more useful for the retention of the clades obtained in the cladistic analysis of his complete dataset than the hard-tissue-based characters). A similar pattern was seen for the consistency index (CI), in which the number of informative myological characters used was significantly higher than that for the informative osteological characters (0.71 and 0.52, respectively). Thus, both of these studies suggested that although osteological structures provide more potential characters for phylogenetic analyses, myological characters

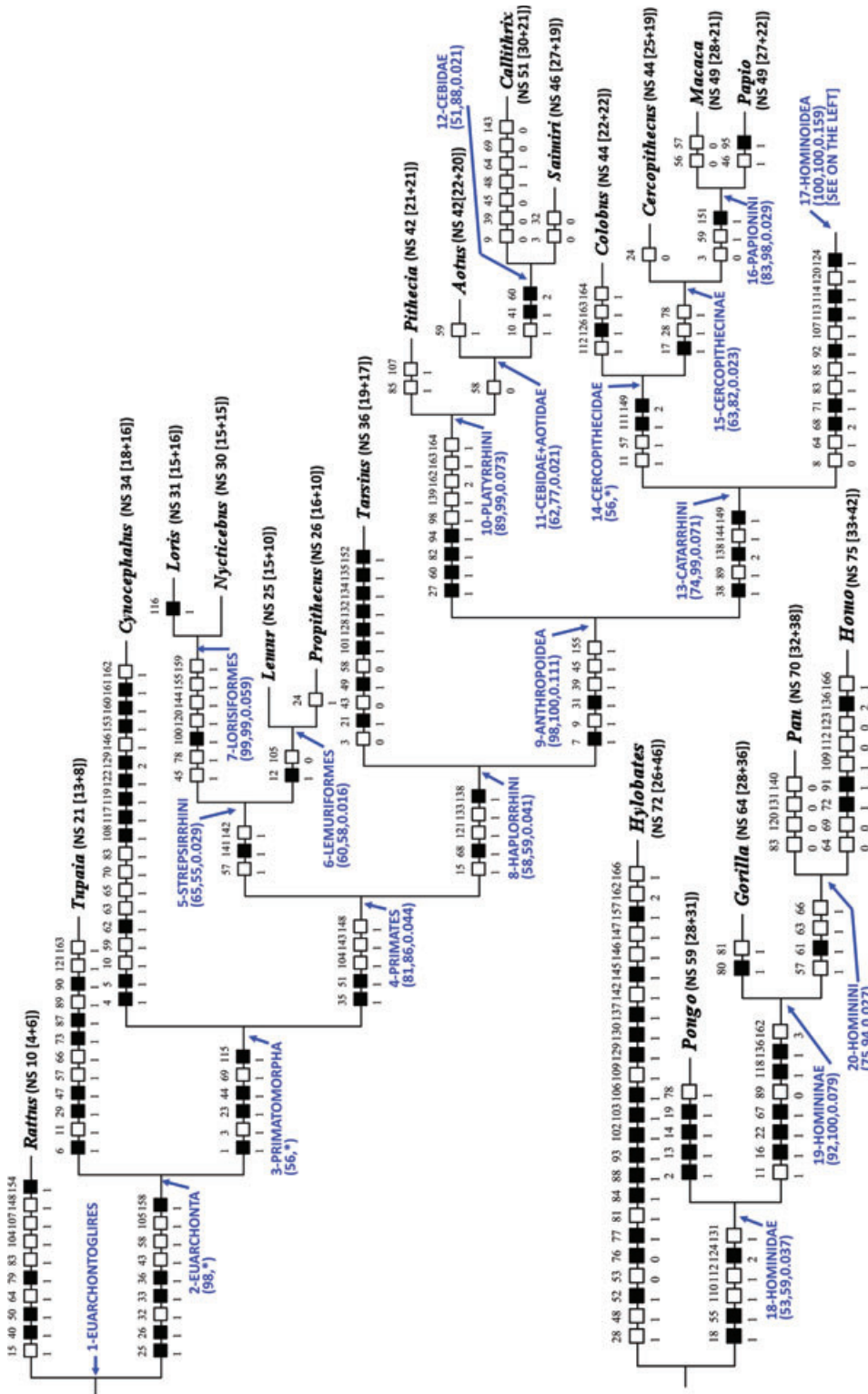


Fig. 1. Single most parsimonious tree (length $L = 301$, consistency index $CI = 58$, retention index $RI = 73$) obtained from the analysis of 166 characters of the primate head, neck, pectoral and forelimb musculature (Diogo & Wood, 2011, 2012a); modified from Diogo & Wood (2011). Unambiguous transitions that occurred in each branch are shown as white (homoplastic transitions) and black (non-homoplastic transitions) squares (numbers above and below the squares indicate the character and character state, respectively). Below the number and name of each clade are shown the bootstrap support values (BSV) obtained from the parsimony analysis (on the left), the credibility support values (CSV, centre) and branch lengths (BL, right; shown when $CSV \geq 50$) obtained from the Bayesian analysis. NS indicates total number of unambiguous evolutionary steps accumulated from basal node of tree to the respective terminal taxa; between square brackets are shown the partial numbers for the head and neck (on the left) and for the pectoral and upper limb (right) characters. * indicates support values that are < 50 , i.e. all clades obtained in the parsimony analysis were also obtained in the Bayesian analysis, excepting that the Bayesian ‘majority consensus’ tree has a trichotomy leading to *Cynocephalus* + *Tupaia* (this clade having a CSV of 53; BL of 0.046), to *Rattus*, and to Primates, and a trichotomy leading to *Colobus*, to the Cercopithecinae, and to hominoids.

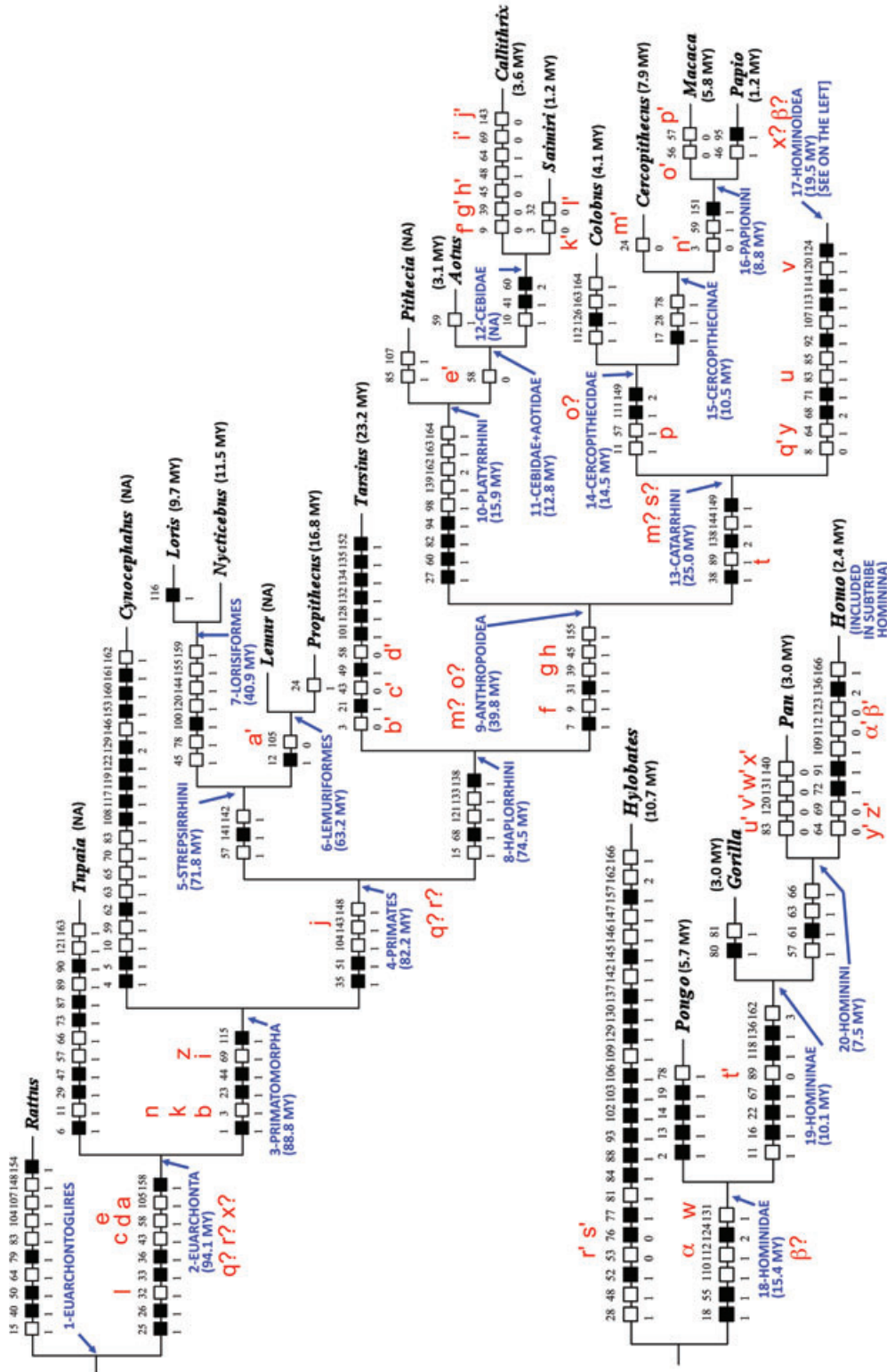


Fig. 2. Single most parsimonious tree (length $L=301$, consistency index $CI=58$, retention index $RI=73$) obtained from the analysis of 166 characters of the primate head, neck, pectoral and forelimb musculature (Diogo & Wood, 2011, 2012b); modified from Diogo & Wood (2012b). The unambiguous transitions that occurred in each branch are shown as white (homoplastic transitions) and black (non-homoplastic transitions) squares (numbers above and below the squares indicate the character and character state, respectively). Together with the name of each euarchontian clade is shown the respective estimated molecular divergence time, except for the genus *Homo* for which is shown a time of origin exclusively based on the fossil record (see text for further details). A detailed description of the 28 unambiguous reversions to a plesiomorphic state is given in Table 1, following the alphabetic order used in this figure (letters/symbols without a prime indicate the nodes where the respective original transitions from the plesiomorphic state to the derived state took place); see also Table 2. MY, million years.

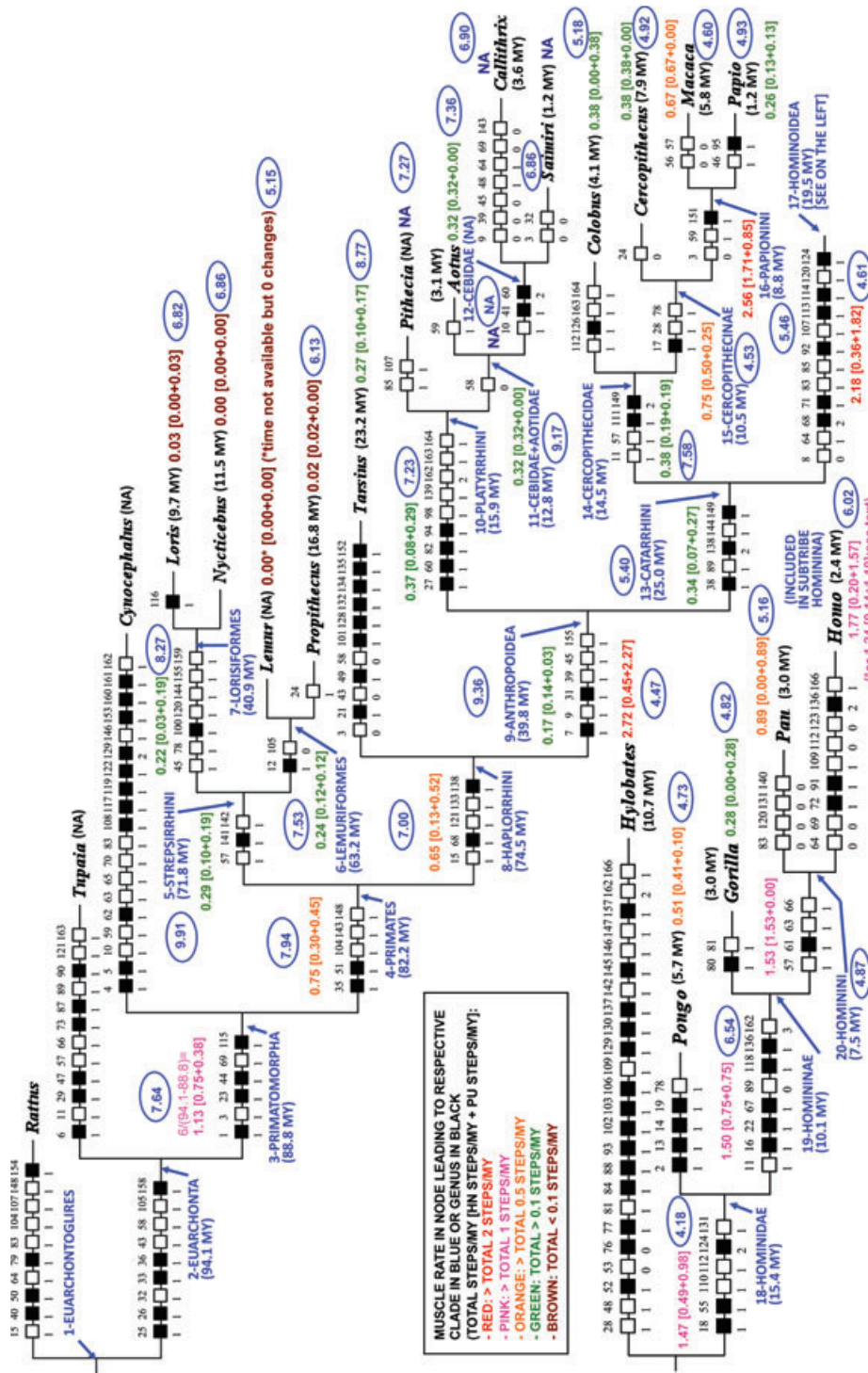


Fig. 3. Single most parsimonious tree (length L = 301, consistency index CI = 58, retention index RI = 73) obtained from the analysis of 166 characters of the primate head, neck, pectoral and forelimb musculature (Diogo & Wood, 2011, 2012a); modified from Diogo *et al.* (in press-d). Unambiguous transitions occurring in each branch are shown as white (homoplastic transitions) and black (non-homoplastic transitions) squares (numbers above and below the squares indicate the character and character state, respectively). For each euarchontan clade we show the respective estimated molecular divergence time based on Fabre *et al.* (2009); the only exception is the genus *Homo* for which we show the consensus first appearance datum based on the fossil record [as *H. sapiens* is the only extant species of this genus we cannot tell whether the character apomorphies listed for *Homo* were already present in the last common ancestor of the various *Homo* species c. 2.4 million years ago (Ma), or whether they accumulated up until the origin of *H. sapiens* c. 200 thousand years ago; so in this case we provide two rates of evolution for the node leading to modern humans, one (1.77) resulting from the division of the nine character state changes accumulated in that node by 5.1 (i.e. 7.5 to 2.4 Ma), the other (1.24) resulting from the division of the nine character states by 7.3 (i.e. 7.5 to 0.2 Ma)]. The taxa for which Fabre *et al.* (2009) only examined a single species (e.g. the genera *Lemur* and *Pithecia*) as well as the family Cebidae (which was not recovered as a monophyletic group by Fabre *et al.*, 2009) are indicated as 'NA' (non applicable). The muscle evolutionary rates [number of total unambiguous character state changes as well as of unambiguous head and neck (HN); characters 1–67] and pectoral and upper limb (PU; characters 68–166) character state changes per 1 million years (1 MY) for each node within the primate clade and for the node leading to these nodes (see text for further details). For comparison, the nucleotide substitution rates (unit = number of substitutions/site/MY × 10⁴; see text for more details) calculated by Perelman *et al.* (2011) is shown inside a blue oval next to each node.

are more useful for inferring the phylogenetic relationships among higher clades. This suggestion has been corroborated in studies that have focused on other major vertebrate groups [e.g. teleosts (Winterbottom, 1974, 1993), hominoids (Gibbs *et al.*, 2002), and dinosaurs (Dilkes, 2000)]. However, there are cases in which the results of myological studies are different from those of molecular works. For instance, Abdala & Moro (2003, 2006) undertook a myological study of 10 squamate families that did not include iguanids, varanids, or snakes, and contrary to molecular studies they did not find geckos to be basal, although their grouping of teiids, lacertids, and gymnophthalmids does agree with molecular studies. McKittrick's (1991) myological study of birds failed to find a monophyletic Galloanserae as the outgroup of Neoaves in the Neognathae and nested galliforms and anseriforms far from each other within neognaths; most osteological trees agree with molecular studies in finding a monophyletic Galloanserae at the base of Neognathae. Also concerning birds, it should be noted that the papers by Livezey & Zusi (2007), which used a more extensive data set with myological characters from the head, neck and pectoral and pelvic regions, has been criticized for deviating significantly from the findings of phylogenetic studies using molecular data [see, e.g. Mayr (2008) for an account on avian higher-level phylogeny].

As part of our long-term project we have recently dissected the head, neck, pectoral and upper limb muscles of representative members of each major extant primate group and of non-primate taxa, including Glires, Dermoptera and Scandentia. The information obtained from our dissections and our review of the literature was coded and used in both parsimony and Bayesian cladistic analyses based on a total of 166 characters and of 21 terminal taxa [18 primate taxa (ingroup) plus *Rattus*, *Cynocephalus* and *Tupaia* (outgroups)]. For lists of the dissected specimens, the 166 characters included in the phylogenetic analyses and the synapomorphies/apomorphies for each of the clades and terminal taxa shown in Figs 1–3 see Diogo & Wood (2011, 2012a). The most parsimonious tree obtained from the analysis of the 166 head, neck, pectoral and upper limb myological characters in the 13 non-hominoid primate genera and in the outgroups (Fig. 1) is congruent with the molecular trees obtained recently by Fabre, Rodrigues & Douzery (2009), Arnold, Matthews & Nunn (2010), and Perelman *et al.* (2011). The only caveat is that in Fabre *et al.*'s (2009) study *Saimiri* (a cebid) is closer to the aotid *Aotus* than to *Callithrix* (another cebid) and in Perelman *et al.*'s (2011) study *Callithrix* is closer to *Aotus* than to *Saimiri*. In our study (Fig. 1) and in Arnold *et al.*'s (2010) study *Saimiri* is closer to *Callithrix* (i.e. the Cebidae are a monophyletic group); these latter results (Fig. 1) are consistent with the most recent molecular-based analyses of platyrrhine phylogeny (Wildman *et al.*, 2009). Most of the major primate clades are supported by high parsimony bootstrap support values (BSV) and/or Bayesian credibility support values (CSV) (e.g. 6 of the 15 non-hominoid primate clades have CSV and/or BSV \geq 8). This is thus the first morphological cladistic study based on

a large data matrix to provide compelling levels of support for the chimp-human clade (BSV 75, CSV 94). Therefore, apart from the utility of mapping myological characters on osteological or molecular phylogenies to address evolutionary questions, the results of our studies of primates and teleosts (as well as of studies of other authors in teleosts, hominoids and dinosaurs: summarized in Diogo & Abdala, 2010, see above) point out that these myological characters can also be useful to generate phylogenies by themselves.

It is often said that one of the drawbacks to using muscular characters is their limitation in phylogenetic studies of fossil taxa. However, in our opinion this criticism applies more to molecular studies, because various studies have shown that muscle characters can be very helpful in inferring the phylogeny of fossil taxa, e.g. of dinosaurs (e.g. Dilkes, 2000). To investigate whether the results of our analysis of primate myology could be used to develop more effective phylogenetic analyses of the primate fossil record, we analyzed a dataset that included only myological characters that might be recovered in fossil taxa (i.e. characters taken from the bony skeleton of the head and neck, upper limb girdle and upper limb: the numbers of the 92 characters included in this dataset are listed in Diogo & Wood, 2011, 2012a). Most of the characters based on the facial and laryngeal muscles were not included in that dataset because these muscles do not usually attach onto bones. With respect to the hominoids, the analysis of the dataset recovered the monophyly of the Hominoidea and Homininae, but the loss of useful variation in the head and neck characters and the homoplasies in the pectoral and upper limb musculature resulted in the grouping of *Hylobates* with the Homininae and of *Gorilla* with *Homo* (N.B., the subtribe Hominina includes all extant and fossil humans and together with the subtribe Panina forms the tribe Hominini, which is included in the subfamily Homininae together with the tribe Gorillini: e.g. Diogo & Wood, 2012a). However, these erroneous groupings had low support values; moreover, among non-hominoid primates the results of analyzing this subset of characters were particularly encouraging: the consensus parsimony tree recovered 12 (80%) of the 15 non-hominoid clades shown in Fig. 1 (Diogo & Wood, 2011).

III. THE IMPORTANCE OF HOMOPLASY AND REVERSIONS IN EVOLUTION AND DOLLO'S LAW

Morphological cladistic analyses based on muscles also allow us to address broader macroevolutionary topics. For example, when we ran separate cladistic analyses of datasets based on the two main anatomical regions we sampled, i.e. the head and neck (HN: characters 1–67) and the pectoral region and the upper limb (PU: characters 68–166), we found that HN muscles are more effective at recovering the molecular evolutionary tree of primates shown in Fig. 1. That is, whereas the consensus tree obtained from the parsimony analysis of 67 HN characters recovered 17 of the 20 clades

shown in the parsimony tree of Fig. 1, the consensus tree obtained from the parsimony analysis of a larger number (i.e. 99) of PU characters only recovered 12 of the 20 clades. However, despite recovering a smaller number of the clades of the molecular tree of Fig. 1 than do the HN characters, the PU muscle characters are particularly effective at recovering relationships at the base of the primate clade (e.g. order Primates and suborder Strepsirrhini). The most parsimonious tree obtained from the analysis of the complete dataset (CI 58, RI 73) has a total length of 301 steps, of which 100

(33%) are non-homoplasic (i.e. they were not independently acquired or reverted elsewhere in the tree) evolutionary transitions (black squares in Fig. 1). Of the 220 steps that are unambiguously optimized in the tree (squares in Fig. 1), 28 (i.e. 13%) are reversions to a plesiomorphic state (Table 1). Taking into account the total number of steps (301) within the tree, the number of characters (166) and the number of muscles (129) represented by the data in the cladistic analysis, there are *c.*1.8 evolutionary transitions per character and *c.* 2.3 evolutionary transitions per muscle studied. When broken

Table 1. List of the 28 reversions shown in Fig. 2

	Description of reversion	Ch. state ch.	Anat. region
a'	Rev. of 'biceps brachii has no bicipital aponeurosis'	[105:1 - > 0]	Arm
b'	Rev. of 'Digastricus anterior is not in contact with its counterpart for most of its length'	[3:1 - > 0]	Head/neck
c'	Rev. of 'Spinotrapezius is not a distinct muscle'	[43:1 - > 0]	Head/neck
d'	Rev. of 'Chondroglossus is present as a distinct bundle of the hyoglossus'	[58:1 - > 0]	Head/neck
e'	Rev. of 'Chondroglossus is present as a distinct bundle of the hyoglossus'	[58:1 - > 0]	Head/neck
f'	Rev. of 'Pterygoideus lateralis has well-differentiated inferior and superior heads'	[9:1 - > 0]	Head/neck
g'	Rev. of 'Depressor anguli oris is a distinct muscle'	[39:1 - > 0]	Head/neck
h'	Rev. of 'Trapezius inserts onto the clavicle'	[45:1 - > 0]	Head/neck
i'	Rev. of 'Rhomboideus major and rhomboideus minor are not distinct muscles'	[69:1 - > 0]	Pectoral
j'	Rev. of 'Opponens pollicis is a distinct muscle'	[143:1 - > 0]	Hand
k'	Rev. of 'Digastricus anterior is not in contact with its counterpart for most of its length'	[3:1 - > 0]	Head/neck
l'	Rev. of 'Frontalis is a distinct muscle'	[32:1 - > 0]	Head/neck
m'	Rev. of 'Sphincter colli profundus is not a distinct muscle' (either the muscle was lost in anthropoids and then reappeared in the Cebidae + Aotidae clade and in <i>Cercopithecus</i> or was lost in <i>Pithecia</i> and catarrhines and then reappeared in <i>Cercopithecus</i>)	[24:1 - > 0]	Head/neck
n'	Rev. of 'Digastricus anterior is not in contact with its counterpart for most of its length'	[3:1 - > 0]	Head/neck
o'	Rev. of 'Cricoaerytenoideus posterior does not meet its counterpart at the dorsal midline' (either the derived condition was acquired in anthropoids and then reverted in <i>Macaca</i> , <i>Hylobates</i> and <i>Pongo</i> or it was acquired in platyrrhines, in hominins and in cercopithecids and then reverted in <i>Macaca</i>)	[56:1 - > 0]	Head/neck
p'	Rev. of 'Geniohyoideus is fused to its counterpart in the midline'	[57:1 - > 0]	Head/neck
q'	Rev. of 'Temporalis has a pars suprazygomatica' (either the derived condition was acquired in Euarchonta and then reverted in <i>Cynocephalus</i> and hominoids, or it was acquired in <i>Tupaia</i> and Primates then reverted in hominoids)	[8:1 - > 0]	Head/neck
r'	Rev. of 'Pterygopharyngeus is not a distinct muscle' (either the derived condition was acquired in Euarchonta and then reverted in <i>Cynocephalus</i> and <i>Hylobates</i> , or it was acquired in <i>Tupaia</i> and Primates and then reverted in <i>Hylobates</i>)	[53:1 - > 0]	Head/neck
s'	Rev. of 'Levator claviculae inserts onto a more medial portion of the clavicle' (derived condition considered to have probably arisen in catarrhines or in other more inclusive clade and then uniquely reverted in <i>Hylobates</i> , but see notes in text)	[76:1 - > 0]	Pectoral
t'	tRev. of 'Latissimus dorsi and teres major are fused'	[89:1 - > 0]	Pectoral
u'	Rev. of 'Pectoralis minor inserts onto the coracoid process'	[83:1 - > 0]	Pectoral
v'	Rev. of 'Epitrochleoanconeus is not a distinct muscle'	[120:1 - > 0]	Forearm
w'	Rev. of 'Contrahentes digitorum are missing'	[131:1 - > 0]	Hand
x'	Rev. of 'Flexores breves profundi are fused with the intermetacarpales, forming the dorsal interosseus' (either the derived condition was acquired in <i>Tupaia</i> , <i>Cynocephalus</i> , platyrrhines and hominoids and then reverted in <i>Pan</i> , or it was acquired in Euarchonta and then reverted in strepsirrhines, <i>Tarsius</i> , cercopithecids and in <i>Pan</i>)	[140:1 - > 0]	Hand
y'	Rev. of 'Anterior portion of sternothyroideus extends anteriorly to the posterior portion of the thyrohyoideus'	[64:1 - > 0]	Head/neck
z'	Rev. of 'rhomboideus major and rhomboideus minor are not distinct muscles'	[69:1 - > 0]	Pectoral
α'	Rev. of 'Tendon of flexor digitorum profundus to digit 1 is vestigial or absent'	[112:1 - > 0]	Forearm
β'	Rev. of 'Flexor carpi radialis originates from the radius' (the muscle originates from the radius in gorillas, chimpanzees and orangutans, but the usual condition for hylobatids is unclear and thus it is also unclear whether a radial origin constitutes a synapomorphy of hominoids or of hominids).	[123:1 - > 0]	Forearm

Anat. region, anatomical region; Ch. state ch., character state change; Rev., reversion. For further details, see text and Diogo & Wood (2012b).

down into HN characters only (characters 1–67), the number of steps is 124 for the 67 characters and 53 muscles analyzed, so there are *c.* 1.9 evolutionary transitions per character and *c.* 2.3 evolutionary transitions per muscle studied; 39 of the 124 steps (i.e. 31%) are non-homoplastic (the number of steps for each character is given in Diogo & Wood, 2011). Of those 124 steps 91 are unambiguously optimized and 16 of these (i.e. 18%) are reversions. Regarding the PU characters (characters 68–166), there are 177 steps for 99 characters and 76 muscles, that is *c.* 1.8 evolutionary changes per character and *c.* 2.3 evolutionary changes per muscle studied. Within those 177 steps, 61 (i.e. 34%) are non-homoplastic and 129 are unambiguously optimized in the tree; 12 of these (i.e. 9%) are reversions. Therefore, although in our parsimony analysis the frequency of reversions within the HN dataset (i.e. 18%, ratio of 0.30 reversions per muscle studied) is twice that within the PU dataset (i.e. 9%, ratio of 0.16 reversions per muscle), the frequency of non-homoplastic changes is much the same within the two datasets: about two-thirds of the changes are homoplastic in both datasets. This result is consistent with a *t*-test of variable character transition rates obtained by us from the Bayesian gamma model and also with a recent analysis of osteological data (Williams, 2007), which revealed that the levels of homoplasy found in the dentition, the cranium, and the postcranium of primates are also essentially similar.

The numbers given above clearly stress the importance of homoplasy and of evolutionary reversions in morphological evolution, a point stressed in Wake's (2009) review of his salamander research. As stressed by Wiens (2011), less attention historically has been given to evolutionary reversions than to the two other types of homoplastic events, parallelism and convergence (see Diogo, 2005). Wiens (2011) listed several examples of violations of Dollo's Law (which states that once a complex structure is lost it is unlikely to be reacquired) including the loss of mandibular teeth in the ancestor of modern frogs > 230 million years (MY) ago and their reappearance in the anuran genus *Gastrotheca* during the last 5–17 MY. In Diogo & Wood (2012*b*) we focused on the implications of our comparative and phylogenetic studies for the understanding of the role played by reversions in primate and human evolutionary history. We stressed that reversions played a substantial role in primate and human evolution because one in seven of the HN and PU 220 evolutionary transitions unambiguously optimized in the tree shown in Figs 1 and 2 are reversions to a plesiomorphic state ($N = 28$) (Fig. 2, Table 1). Of those 28 reversions, 6 played a direct role in our own evolution, for they occurred at the nodes that lead to the origin of modern humans. Moreover, 9 of those 28 reversions violate Dollo's law, with the average time between a structure's loss and reacquisition being *c.* 51 MY (Fig. 2; Table 2; see Diogo & Wood, 2012*b*).

Our comparative analyses provide evidence to support the hypothesis that the reacquisition in adults of anatomical structures that were missing for long periods of time is because the developmental pathways responsible were maintained in the members of that clade. An example

of this concerns the presence/absence of the *contrahentes digitorum* muscles in adult hominids. Chimpanzees display a reversion (character 131: $1 > 0$) of a synapomorphy of the Hominidae (acquired at least 15.4 MY ago: Fig. 2 and Tables 1 and 2) in which adult individuals have two *contrahentes digitorum* (in adults of other hominid taxa there are usually none) other than the muscle *adductor pollicis*, one going to digit 4 and the other to digit 5. Studies of the development of hand muscles (e.g. Cihak, 1972) have shown that karyotypically normal modern human embryos do have *contrahentes* going to various fingers, but the muscles are lost during later embryonic development. Moreover, other studies (e.g. Dunlap, Aziz & Rosenbaum, 1986) have shown that in karyotypically abnormal modern humans, such as individuals with trisomies 13, 18 or 21, the *contrahentes* muscles often persist until well after birth. The presence of the *contrahentes* in adult chimpanzees is thus probably related to the occurrence of heterochronic, and specifically paedomorphic events in the lineage leading to the genus *Pan*. Similarly, the evolutionary reversion leading to the presence of distinct intermetacarpals in adult chimpanzees is probably also related to paedomorphic events for Cihak (1972) has shown that the muscles intermetacarpals are also present as distinct muscles in early embryos of karyotypically normal modern humans. Thus, there is evidence that at least some of the evolutionary reversions that violate Dollo's law involve the maintenance of ancestral developmental pathways ('hidden variation') (see also, e.g. Gould, 1977; Alberch, 1989; Wiens, 2011). The 'hidden variation' and thus the maintenance of these pathways is likely associated with internal developmental constraints (e.g. the persistence of the *contrahentes* to digit 1, or 'adductor pollicis', in karyotypically normal modern humans is enabled by the formation of the full set of *contrahentes* early in ontogeny; the other *contrahentes* are then lost during normal development). Many developmental pathways are involved in the formation of more than one anatomical structure, and selection may maintain them for this reason (Gould, 2002). It is important to emphasize that these are not cases of recapitulation in the Haeckelian sense. For example, the *contrahentes digitorum* and the intermetacarpals of karyotypically 'normal' modern human embryos do not correspond to the muscles of adult primates such as chimpanzees and of other primate/mammalian adults, but instead to the muscles of the embryos of the latter taxa.

IV. THE DIRECTIONALITY OF EVOLUTION AND THE MYTH OF HUMAN COMPLEXITY

Other macroevolutionary topics that can be addressed using the results of our cladistic analyses of primate myological characters are those more directly related to the evolution of our own clade, Hominina (see Figs 1, 2 and 3). Bakewell, Shi & Zhang (2007, p. 7492) state that their molecular studies show that 'in sharp contrast to common belief, there were more adaptive genetic changes during chimp

Table 2. Time frame over which lost traits were regained within the euarchontan clade according to our phylogenetic study (see Figs 1 and 2) and using the estimate times provided by Fabre *et al.* (2009)

Structure that was regained, violating Dollo's law (letters shown before the description of each structure correspond to letters shown in Fig. 2)	Number of evolutionary steps according to the hypothesis that violates Dollo's law (in bold) <i>vs</i> number of evolutionary steps that one would need to assume in order to not violate Dollo's law (in non-bold, following the description of these steps)	Date when feature was lost (*)	Date when feature was regained (**)	Time passed between (*) and (**)
(a') Bicipital aponeurosis (N.B., in modern humans the bicipital aponeurosis helps to reinforce the cubital fossa and to protect the branchial artery and the median nerve running underneath)	2 <i>vs</i> 4 (loss in <i>Tupaia</i> , <i>Cynocephalus</i> , lorisiforms and haplorrhines)	94.1 MY	63.2 MY	30.9 MY
(c') Spinotrapezius (N.B., the spinotrapezius is a separate muscle that corresponds to the descending part of the trapezius of modern humans, which mainly depresses the scapula)	2 <i>vs</i> 4 (loss in <i>Tupaia</i> , <i>Cynocephalus</i> , strepsirrhines and anthropoids)	94.1 MY	23.2 MY	70.9 MY
(i') Rhomboideus minor (N.B., in modern humans the rhomboideus minor acts together with the rhomboideus major to adduct the scapula and keep the scapula pressed against the thoracic wall)	3 <i>vs</i> 10 (loss in <i>Tupaia</i> , <i>Cynocephalus</i> , tarsiers, <i>Pithecia</i> , <i>Aotus</i> , <i>Saimiri</i> , hylobatids, orangs, gorillas and chimps: see text)	88.8 MY	3.6 MY	85.2 MY
(m') Sphincter colli profundus (N.B., the sphincter colli profundus is a thin facial muscle that lies deep to the platysma cervicale)	3 <i>vs</i> 4 (loss in <i>Pithecia</i> , <i>Colobus</i> , Papionini and hominoidea)	39.8 MY or 25.0 MY	7.9 MY	31.9 MY or 17.1 MY (mean = 24.5 MY)
(r') Pterygopharyngeus (N.B., the pterygopharyngeus might correspond to the pterygopharyngeal part of the superior pharyngeal constrictor of modern humans, which connects the medial pterygoid plate and its hamulus to the median raphe and mainly acts together with the other parts of the muscle to constrict the pharynx)	3 <i>vs</i> 6 (loss in <i>Tupaia</i> , strepsirrhines, tarsiers, platyrrhines, cercopithecids, and hominoids)	94.1 MY or 82.2 MY	10.7 MY	83.4 MY or 71.5 MY (mean = 77.4 MY)
(v') Epitrochleoanconeus (N.B., the epitrochleoanconeus mainly connects the medial epicondyle of the humerus to the olecranon process of the ulna, so it potentially helps to extend the forearm and/or stabilize the elbow joint)	2 <i>vs</i> 4 (loss in hylobatids, orangs, gorillas and Hominina)	19.5 MY	3.0 MY	16.5 MY
(w') Contrahentes digitorum (N.B., the contrahentes adduct the digits; see text)	2 <i>vs</i> 3 (loss in orangs, gorillas and Hominina)	15.4 MY	3.0 MY	12.4 MY
(x') Intermetacarpales (N.B., the intermetacarpales connect the metacarpals of adjacent digits; see text)	5 <i>vs</i> 7 (loss in <i>Tupaia</i> , <i>Cynocephalus</i> , platyrrhines, hylobatids, orangs, gorillas and Hominina)	94.1 MY or 19.5 MY	3.0 MY	91.1 MY or 16.5 MY (mean = 53.8 MY)
(z') Rhomboideus minor (N.B., in modern humans the rhomboideus minor acts together with the rhomboideus major to adduct the scapula and keep the scapula pressed against the thoracic wall)	3 <i>vs</i> 10 (loss in <i>Cynocephalus</i> , strepsirrhines, tarsiers, <i>Pithecia</i> , <i>Aotus</i> , <i>Saimiri</i> , hylobatids, orangs, gorillas and chimps: see text)	88.8 MY	2.4 MY	86.4 MY
				Total mean: 50.9 MY

N.B., the approximate time of origin of the genus *Homo*, 2.4 million years (MY) (for further details, see text and Diogo & Wood, 2012b).

evolution than during human evolution' and they claim that their analysis 'suggests more unidentified phenotypic adaptations in chimps than in humans'. The results of our primate parsimony and Bayesian analyses based on muscles indicate that, at least regarding the gross morphology of the HN and musculature, since the *Pan/Homo* split the clade Hominina has evolved faster than the panin clade [*c.* 2.3 times faster according to the lengths of the branches leading to modern humans (9) and to chimpanzees (4) in the parsimony tree of Fig. 1]. In turn, since the split between *Gorilla* and the Hominini, gorillas have only accumulated

two unambiguous muscular apomorphies, whereas there are 8 (4 + 4) and 13 (4 + 9) unambiguous apomorphies leading to extant chimpanzees and to modern humans, respectively (Fig. 1). In terms of their significance for our understanding of human evolution, our results could seem paradoxical. On the one hand the cladistic analyses suggest there are more unambiguous evolutionary steps (NS) from the base of the tree to modern humans than to any other taxon included in the study (Fig. 1). But, on the other hand, our comparative anatomical studies show that modern humans have fewer muscles than most other primates, including chimpanzees,

and have many fewer muscles than do strepsirrhines and tarsiiiforms (see Diogo & Wood, 2011).

Gould noted in *'The Structure of Evolutionary History'* (2002) that 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 un-reported or under-reported because stasis is interpreted as 'no data'. The results of our study support Gould's (2002) contention in the sense that there is no general trend to increase the number of muscles, or muscle bundles, 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 the cladistic study (Fig. 1) these evolutionary transitions did not result in more muscles, or more muscle components (see Diogo *et al.*, 2008, 2009*a,b*, 2010; Diogo & Abdala, 2010; Diogo & Wood, 2011, 2012*a*). For example, although some of the nine modern human apomorphies acquired since the *Pan/Homo* split (Fig. 1) involve the differentiation of new muscles [rhomboideus major and rhomboideus minor (character 69), extensor pollicis brevis (character 166) and flexor pollicis longus (character 109)], others involve the loss of muscles [levator claviculae (character 72) and dorsoepitrochlearis (char 91)]. As a result, more muscle changes were accumulated in our evolutionary history than in that of modern chimpanzees but there are usually more head and neck and pectoral and upper limb muscles present in modern chimpanzees than in members of our own species (normally 126 in the former *versus* 123 in the latter: see Diogo & Wood, 2011, 2012*a*). In fact, with respect to the number of HN and PU muscles and muscle bundles, once could make the case that modern humans are relatively simplified mammals (Diogo & Abdala, 2010).

V. TEMPO AND MODE OF PRIMATE AND HUMAN EVOLUTIONARY HISTORY

Recent studies suggest that rates of both morphological and molecular evolution vary among taxa (e.g. Chatterjee *et al.*, 2009; Cooper & Purvis, 2009; Perelman *et al.*, 2011). The occurrence of different molecular rates is consistent with the concept of local molecular clocks. According to Tetushkin (2003, p. 729), primates 'provide the most interesting and striking example of such heterogeneity in the tempo of molecular evolution'. Most recent studies dealing with evolutionary rates within mammals are based on molecular evidence; the few that are non-molecular do not focus on detailed morphology, but mainly on global features of the phenotype such as body size (see Venditti, Meade & Pagel, 2011, for a recent review). We calculated the rates of muscle evolutionary change within the primate clades resulting from our myology-based cladistic analyses (Diogo *et al.*, in press-*a*; Fig. 3) and compared them with the molecular rates obtained by other authors, including the rates of molecular nucleotide substitution reported by Perelman *et al.* (2011). We addressed

the following questions: (i) are the rates of muscle evolution the same or different across different primate taxa and across different geological time-periods; (ii) are the muscle rates more in agreement with the gradualist model, with the punctuated equilibrium model, or with other models of evolutionary rate; and (iii) are the muscle rates in general similar to the molecular rates provided in recent papers, or is there a mismatch between morphological and molecular rates as predicted by the neutral evolution model of Kimura (1968)?

We found several examples of gradualism during which the rates of various lineages of each of the major primate clades are strikingly similar. For instance, the rate of muscle evolution at the node leading to the clade including the platyrrhine families Cebidae plus Aotidae (0.32) is the same as that at the node leading to a single aotid genus, *Aotus* (0.32), and is similar to that at the node leading to the whole Platyrrhini clade (0.37) (Fig. 3). Moreover, the rate at the node leading to the Cercopithecidae (0.38) is the same as that at the node leading to the cercopithecoid *Colobus* (0.38) and at the node leading to *Cercopithecus* (0.38) (Fig. 3). As these are the only rates that are similar across the whole tree set out in Fig. 3, and as this happens inside two different clades (New and Old World monkeys), it seems that for some reason the number of morphological evolutionary changes accumulated per period of time in at least some nodes within a clade is essentially constant. This would be the expectation for molecular evolutionary changes according to the neutral model of evolution, but this has not been reported previously for any type of morphological evolutionary changes, at least within the order Primates. Moreover, the muscle rate at the node leading to strepsirrhines (0.29) and then at the subsequent nodes leading to the lorisiiforms (0.22) and to the lemuriforms (0.24) are also very similar to each other, particularly when one compares the differences with the range of different rates within all the primate nodes shown in Fig. 3 (0.00–2.72). The same can be said about the rates at the nodes leading to the Hominoidea (1.47), Hominoidea (1.50) and Hominiini (1.53) (Fig. 3). These results therefore seem to support the proposal by authors such as Gould (2002) that 'internal' (e.g. ontogenetic) constraints play an important role in evolution. That is, in the last 25 Ma there have been major climate and environmental changes in Africa and Asia, yet the rate of muscle changes accumulated during that period at the nodes leading to the Cercopithecidae and then to *Colobus*, and also to *Cercopithecus*, is exactly the same. These similarities in overall rates do not necessarily correspond to similarities in the rates for the HN and PU regions. At the node leading to the Cercopithecidae the rate for the HN changes is 0.19, at the node leading to *Colobus* it is 0.00, and at the node leading to *Cercopithecus* it is 0.38: the respective rates for the PU region are 0.19, 0.38 and 0.00.

For those authors that support the paradigm of 'internal constraints' the analysis of these partial rates would be viewed as evidence that ontogenetic constraints are so strong and interconnected that the potential for overall change accumulated in the different regions of the body is limited.

This is in line with the results of recent studies showing that in early organogenesis, and particularly during the so-called ‘phylotypic stage’, there is substantial interactivity among different body modules and thus there is low effective modularity (e.g. Galis & Metz, 2007). It has also been argued that from a developmental perspective, if extensive somatic investment is made in one structure of one body module, this could limit investment dedicated to the formation of another structure from not only that module but also from other body modules; it is also possible that constructional trade-offs constrain investment in whole phenotypes because the structural space in organisms is limiting (e.g. Hulsey & Hollingsworth, 2011).

However, our study also provides examples of a shift towards a faster rate of muscle evolution that is then followed by a slow down in the rate of muscle evolution (i.e. a punctuated equilibrium mode). With respect to the third question raised above, there are several examples of substantial differences between muscle and molecular evolutionary rates at the same primate nodes, as would be predicted by the neutral model of evolution. But at other places on the tree the muscle evolutionary rates obtained in our study are similar to the published rates of molecular evolution. In summary, our study suggests that the tempo and mode of primate and human evolution is complex, and provides examples of different modes of evolution within the Primate clade. It suggests that at the level of such major mammalian and probably vertebrate clades, simplistic dichotomies such as ‘gradual *versus* punctuated’ and ‘neutral *versus* non-neutral’ do not apply. Also, contrary to the idea of a ‘general molecular slow-down of hominoids’, the muscle evolutionary rates at the nodes leading to, or within, the hominoids are among the highest within the whole Primate clade.

VI. ADAPTIVE RADIATIONS AND THE NOTION OF ‘COMMON IS PRIMITIVE’

Sallan & Friedman (2012) suggest that adaptive radiations, which are bouts of morphological divergence coupled with taxonomic proliferation, underpin biodiversity. The most widespread model of adaptive radiations assumes a single round, or ‘early burst’, of elevated phenotypic divergence followed by a decline in rates of change or even stasis (Sallan & Friedman, 2012). A vertebrate-specific model proposes separate stages: initial divergence in postcranial traits related to habitat use, followed by diversification in cranial morphology linked to trophic demands. However, according to these authors there is little empirical evidence for either hypothesis. In fact, based on their own studies they state that, contrary to both models, separate large-scale radiations of actinopterygian fishes proceeded through distinct cranial and later postcranial stages of morphological diversification. A relevant question we can address with our primate data is: are the evolutionary rates of the HN muscles higher or lower than those of the PU muscles?

If one takes into account the rates shown in Fig. 3 for each of the 31 primate nodes for which rates are available (thus not including the nodes leading to *Pithecia*, to the Cebidae, to *Callithrix* and to *Saimiri*; N.B., also not including the node leading to the order Primates as a whole), the average rate of HN changes per node per million years (MY) is 0.297 (i.e. the sum of HN rates for the 31 nodes = 9.20) and the average rate of PU changes per node per MY is 0.396 (i.e. the sum of PU rates for the 31 nodes = 12.27). Thus, the average PU rate is slightly more than 1.3 times greater than the average HN rate. But this difference is much greater if one considers just the nodes that lead to the four major primate clades (i.e. Strepsirrhini, Platyrrhini, Cercopithecidae and Hominoidea). At these nodes the average rate of HN changes per node per MY is 0.182 (total sum of HN rates for the four nodes = 0.73) and the average rate of PU changes per node per MY is 0.622 (total sum of PU rates for the four nodes = 2.49). This means that the ratio of the PU rate to the HN rate (3.418) at these four nodes is more than twice that (2.36 times to be exact) at the 31 primate nodes for which the rates are available. In other words, during the evolutionary events that led to the four major primate clades the PU muscles were evolving at a relatively higher rate (compared to the HN muscles). Our myological data thus lend support to the ‘vertebrate-specific model’ described above in the sense that during the genesis of the major primate phenotypes there was a particular emphasis on ‘habitat divergence’ (mainly defined by postcranial changes related to locomotion) and not on ‘trophic divergence’ (mainly defined by cranial changes related to feeding). We hope these preliminary data will stimulate others to consider the role myological data could play in discussions about these macroevolutionary questions (Sallan & Friedman, 2012).

A widely held assumption that can be tested with our myological data is that ‘common is primitive’, which has often been criticized as unsupported and rejected as a criterion for determining character polarity (e.g. Watrous & Wheller, 1981; Wiley, 1981). However, the computer simulations carried out by Wiens (1998, p. 397) suggested that in many cases ‘common is primitive’ does seem to be a valid assumption, particularly in cases of ‘low and intermediate rates of character change’. According to Wiens (1998) this observation may have applications to situations where the ancestral state of a higher taxon with unresolved internal relationships is sought and/or in outgroup analysis when outgroup relationships are unresolved. A simple way of testing this using the results of our primate cladistic analysis is to count the number of characters for which the character state that is most common in the sampled 21 taxa corresponds to the character state that is considered to be the most primitive one for the whole according to the results of the phylogenetic analysis. Of the 166 characters considered in the Diogo & Wood (2011) analysis, there are 132 for which the plesiomorphic state for the whole group can be unambiguously assigned (the 34 characters in which this is not the case are characters 2, 7, 13, 33, 37, 39, 40, 42, 46, 48, 50, 53, 54, 56, 59, 62, 63, 64, 65, 71, 82, 86, 89, 92,

108, 109, 120, 137, 146, 151, 153, 156, 157, and 159). Of these 132 characters, in one (character 75) a similar number of taxa (10) display character states 0 and 1 (the other taxon within the 21 taxa was coded as inapplicable). Among the remaining 131 characters, in 98 the state most commonly found in the 21 taxa corresponds to the most primitive state for the whole group (the 33 exceptions being characters 1, 3, 8, 9, 15, 20, 23, 25, 26, 31, 32, 35, 36, 43, 44, 45, 51, 58, 68, 69, 99, 104, 105, 115, 121, 133, 138, 143, 144, 148, 150, 155, and 158). Therefore, in c. 75% of the eligible characters (i.e. 98 out of 131) in our study the assumption that ‘common is primitive’ is valid.

VII. MORPHOGENESIS AND VARIATION AMONG HEAD, NECK, PECTORAL AND UPPER LIMB MUSCLES

Developmental studies carried out in recent years have shown there are important differences in the expression patterns associated with morphogenesis of the forelimb and of the hindlimb and between proximal and distal regions within each limb. For example, *Hox9* paralogs are active in the arm but not in the thigh (see fig. 1 of Young & Hallgrímsson, 2005) and studies have also shown that the formation of the muscles of the proximal forelimb occurs through mechanisms that are markedly different from those leading to the formation of the muscles of the distal forelimb (i.e. of the arm, forearm and hand muscles, which arise through classic and well-studied migration from the somites to the limb bud). The superficial girdle muscles (‘appendicular pectoral girdle muscles’ *sensu* Diogo & Abdala, 2010, e.g. pectoralis major and latissimus dorsi) develop by an ‘in-out’ mechanism whereby migration of myogenic cells from the somites into the limb bud is followed by their extension from the proximal limb bud out onto the thorax, and the deep girdle muscles (‘axial pectoral girdle muscles’ *sensu* Diogo & Abdala, 2010, e.g. rhomboideus, serratus anterior) are induced by the forelimb field that promotes myotomal extension directly from the somites (Valasek *et al.*, 2011). According to Valasek *et al.* (2011) the appearance of the forelimb is followed by pectoral girdle development that braces the distal limb to the axial skeleton; the limb program was able to induce and recruit axial structures for its anchorage – the medial scapular border in mammals and the scapular blade in birds (as well as the deep girdle muscles and possibly even the cleithrum and sternum, according to them). The ‘in-out’ mechanism has already proven useful to help understand why in the evolution of the peculiar body shape of turtles the superficial girdle muscles changed their proximal origin while the deep girdle muscles changed their distal insertion (Nagashima *et al.*, 2009). Another important difference between the proximal limb and the distal limb is that in the proximal limb tendons are induced but do not segregate to form specific tendons in the absence of muscles, while in the distal limb (e.g. autopod), where muscles are only present at later ontogenetic stages, tendon formation is initiated and

segregation into individual tendons occurs in the absence of muscles. These distal tendons will however later require muscle contact, and will degenerate in a muscle-less limb environment (Hasson, 2011).

Our cladistic analyses allow us to test directly some of the hypotheses advanced by these and other authors about the morphogenesis of the pectoral and upper limb muscles. For example, if the ‘in-out’ *versus* ‘myotomal extension’ morphogenetic hypothesis elaborated by Valasek *et al.* (2011) applies to clades such as primates, one would expect that the superficial (appendicular) pectoral girdle muscles would accumulate more changes at their proximal origin and that the deep (axial) pectoral girdle muscles would accumulate more changes at their distal insertion, as they did during the evolutionary history of turtles. Within all of the evolutionary changes (steps) listed in the cladistic analysis of primate muscles (Diogo & Wood, 2011), there are 19 changes for a total of 8 deep (axial) pectoral muscles (i.e. serratus anterior, rhomboideus major, rhomboideus minor, rhomboideus occipitalis, levator scapulae, levator clavicularis, subclavius and atlantoscapularis posticus), that is an average of 2.38 character state changes per muscle (see appendix 1 in Diogo & Wood, 2011). Of these 19 changes in the 8 muscles, 2 concern changes in proximal attachments (one in character 71 + one in character 77), so 0.25 per muscle, and 5 concern changes in distal attachments (one in character 74 + three in character 75 + one in character 76), so 0.62 per muscle. That is, within these deep (axial) pectoral muscles, there is a higher rate of change in the distal than in the proximal attachments, thus supporting the hypothesis of Valasek *et al.* (2011). Regarding the superficial (appendicular) pectoral muscles, there are 26 changes for a total of 12 muscles (pectoralis major, pectoralis minor, pectoralis tertius, panniculus carnosus, infraspinatus, supraspinatus, deltoideus scapularis, deltoideus acromialis et clavicularis, teres minor, subscapularis, teres major and latissimus dorsi), that is an average of 2.17 character state changes per muscle (see appendix 1 in Diogo & Wood, 2011). Within these 26 changes in the 12 muscles, 4 concern the proximal attachments (4 in character 78), so 0.33 per muscle, and 8 concern the distal attachments (one in character 80 + six in character 83 + one in character 84), so 0.67 per muscle. That is, within these superficial (appendicular) pectoral muscles, there is also a higher rate of change in the distal attachments than in the proximal attachments. This evidence contradicts the hypothesis of Valasek *et al.* (2011). However, because the changes in proximal attachments relate to ribs and vertebrae they are more difficult to polarize and codify than changes in the distal attachments. The real rate of change per muscle of the proximal attachments of both the deep and the superficial pectoral muscles are therefore very likely greater than the rate cited, and thus it would not be prudent to use these data to contradict Valasek *et al.*’s (2011) hypothesis.

However, because coding bias concerns the proximal attachments of both the deep and the superficial muscles of all taxa, we can more reliably compare the rate of change per muscle for these two types of muscles, which, as noted

above, are 2.38 and 2.17 changes per muscle, respectively. These rates are similar to the rate of 1.95 for the hand muscles (72 changes for a total of 37 muscles), but they are substantially smaller than the rate of 6.4 for the arm muscles (32 changes for a total of 5 muscles) and higher than the rate of 1.24 for the forearm muscles (26 changes for a total of 21 muscles) (see appendix 1 in Diogo & Wood, 2011). Thus, our study of primate muscles does not support the suggestion that the structures of the distal limb, due to their later development and their being contingent on earlier-developing more proximal elements, are more morphologically variable than more proximally located ones (Weisbecker, 2011).

The last example of a hypothesis that can be tested using our primate myological data is that of Lewis (1989) about the relative constancy of muscle attachments. He made the suggestion that ‘while homologous (limb) muscles may show a wide range of shifting origins their insertions tend to remain relatively constant’ (Lewis, 1989, p. 43). This suggestion is not supported by our data, because within the 301 character stage changes of the tree shown in Fig. 1, 48 concern a shift of the distal attachment(s) of the PU muscles whereas only 30 involve a shift of the proximal attachment(s) of these muscles (see appendix 1 in Diogo & Wood, 2011). Within the HN muscles the number of changes concerning a shift of the insertions (i.e. of the attachments onto more movable skeletal structures) is 14, and is remarkably similar to 15, which is the number of changes concerning a shift of their origins.

VIII. CONCLUSIONS

(1) Muscle and other soft tissue evidence has been neglected in systematics and evolutionary biology, but some of the few cladistic analyses based on soft tissues that have been published have shown that these tissues can be useful for inferring phylogenetic relationships, including those among fossil taxa.

(2) The inclusion of soft-tissue-based information in phylogenetic investigations allows researchers to address evolutionary questions that are not tractable using molecular evidence, including crucial questions about the evolution of the closest living relatives of modern humans and evolution within our own clade.

(3) For example, the results of our study stress the importance of homoplasy and of evolutionary reversions in morphological evolution, and provide examples of reversions that clearly violate Dollo’s law.

(4) They also suggest that, contrary to the idea of a ‘general molecular slow-down of hominoids’, the rates of muscle evolution at the nodes leading to the hominoid clade, and those within it, are higher than those in the vast majority of other primate clades.

(5) However, there is no general trend or ‘directionality’ towards increasing complexity during the evolutionary history of hominoids, or of modern humans in particular, at least regarding the number of muscles or muscle bundles.

(6) The rates of muscle evolution at the major euarchontan and primate nodes are different, but within each major primate clade (Strepsirrhini, Platyrrhini, Cercopithecidae and Hominoidea) the rates at the various nodes, and particularly at the nodes leading to the higher groups (i.e. including more than one genus) are strikingly similar.

(7) Our results also support, in general terms, the assumption that ‘common is primitive’ and lend some support to the ‘vertebrate-specific model’ in the sense that they indicate that during the divergent events leading to the four major primate phenotypic lines there was a particular emphasis on postcranial changes and not on cranial changes.

(8) They do not, however, support the suggestion that the distal structures of the upper limb are more morphologically variable than the more proximal ones, nor the idea that there are in general more changes in the origins than in the insertions of the upper limb muscles during evolution.

(9) In the last few decades the emergence of evolutionary developmental biology has resulted in a resurgence of interest in comparative anatomy (e.g. Assis, 2009). We suggest that the forthcoming decades will see a renaissance in the use of myology in evolutionary biology, comparative anatomy and systematics.

(10) This review will hopefully contribute to the knowledge of morphological evolution and in particular to this renaissance by stimulating an interest in the study of muscles. A line of future investigation that is particularly promising is to marry the data obtained from myological studies with palaeontological and environmental data in order to understand better how, where, when and why the anatomical muscle changes occurred.

IX. REFERENCES

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