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VIOLATION OF DOLLO'S LAW: EVIDENCE OF MUSCLE REVERSIONS IN PRIMATE PHYLOGENY AND THEIR IMPLICATIONS FOR THE UNDERSTANDING OF THE ONTOGENY, EVOLUTION, AND ANATOMICAL VARIATIONS OF MODERN HUMANS

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According to Dollo's law, once a complex structure is lost it is unlikely to be reacquired. In this article, we report new data obtained from our myology-based cladistic analyses of primate phylogeny, which provide evidence of anatomical reversions violating Dollo's law: of the 220 character state changes unambiguously optimized in the most parsimonious primate tree, 28 (13%) are evolutionary reversions, and of these 28 reversions six (21%) occurred in the nodes that lead to the origin of modern humans; nine (32%) violate Dollo's law. In some of these nine cases, the structures that were lost in adults of the last common ancestor and are absent in adults of most subgroups of a clade are actually present in early ontogenetic stages of karyotypically normal individuals as well as in later ontogenetic stages of karyotypically abnormal members of those subgroups. Violations of Dollo's law may thus result from the maintenance of ancestral developmental pathways during long periods of trait absence preceding the reacquisition of the trait through paedomorphic events. For instance, the presence of contrahentes and intermetacarpales in adult chimpanzees is likely due to a prolonged/delayed development of the hand musculature, that is, in this case chimpanzees are more neotenic than modern humans.

KEY WORDS: Anatomy, Dollo's law, muscles, phylogeny, primates, reversions, variations.

Dollo's law states that once a complex structure is lost it is unlikely to be reacquired (e.g., Gould 1977, 2002). In a recent paper Wiens (2011; see, e.g., his Table 2) listed several examples of violations of Dollo's law, including the loss of mandibular teeth in the ancestor of modern frogs >230 million years (MY) ago and their reappearance in the frog genus *Gastrotheca* during the

last 5–17 MY, the reappearance of a larval stage in plethodontid salamanders and in hemiphractid frogs, the reappearance of digits in amphisbaeninan lizards of the genus *Bipes*, in gymnophthalmid lizards of the genus *Tretioscincus* and of the genus *Bachia* and in scincid lizards of the genus *Scelotes*, the reappearance of eggshell in the boid snake *Eryx*, and the reappearance of shell

coiling in snails. However, none of the examples cited in Wiens survey involves muscles. This is in large measure because most studies about the evolution of tetrapods and of other vertebrates have been based on hard tissue data.

To address the paucity of data on soft tissues such as muscle, Diogo and colleagues have recently reported the latest results of their long-term study of the comparative anatomy, homologies, and evolution of the head, neck, pectoral, and forelimb muscles of all major groups of nonprimate vertebrates and of primates based on dissection of hundreds of specimens and on a review of the literature (Diogo et al. 2008, 2009a,b, 2010; Diogo and Abdala 2010; Diogo and Wood 2011, 2012). Diogo and Wood (2011) combined data from their dissections with carefully validated information from the literature to undertake the first comprehensive parsimony and Bayesian cladistic analyses of the order primates based on myological data for each of the major primate higher taxa and for a range of outgroups (tree-shrews, dermopterans, and rodents) (Fig. 1). The most parsimonious tree obtained from the cladistic analysis of 166 characters taken from the head, neck, pectoral, and upper limb musculature is fully congruent with Arnold et al.'s (2010) evolutionary molecular tree of primates and similar to the primate molecular trees obtained by Fabre et al. (2009) and Perelman et al. (2011) with the exception that the two latter studies did not recover the Cebidae as a monophyletic taxon (Fig. 1). The results of Diogo and Wood (2011) as well of the other few cladistic analyses based on soft tissues that have been published to date reveal that soft tissues can be particularly useful for inferring phylogenetic relationships, including those among fossil taxa such as dinosaurs; in those cases where the homoplasy of muscles and of hard tissues has been directly compared, in general the former tend to be less homoplastic than the latter (for a recent review, see Diogo and Abdala, 2010). In addition, the inclusion of soft tissue-based information in phylogenetic investigations allows researchers to address evolutionary questions that are not tractable using other types of evidence, including questions about the evolution and functional morphology of, as well as the occurrence of homoplasy (including evolutionary reversions) and of neotenic features in, our closest living relatives and our own clade (Diogo and Wood, 2012).

In the present article, we report new data obtained from our myology-based cladistic analyses regarding the occurrence of evolutionary reversion that violate and that do not violate Dollo's law within the primate clade and discuss the time frame over which lost traits were regained within this clade. We also explore the implications of our comparative and phylogenetic studies for the understanding of the evolution, ontogeny, and variability of primates and of modern humans and particularly of the role played by reversions in primate and human evolutionary history.

Materials and Methods

The nomenclature for the head, neck, pectoral, and upper limb muscles follows that of Diogo and Abdala (2010). The discussions of the muscle evolutionary changes occurring in each of the nodes shown in the tree of Figure 1 and mentioned in the text and in Tables 1 and 2 are based on the phylogenetic results of the myology-based Bayesian and parsimonious cladistic analyses of Diogo and Wood (2011; see Appendix). The estimated divergence times for the euarchontan taxa shown in that tree follow Fabre et al. (2009). The times shown for each taxon refer to the divergence times of the most distantly related species included in Fabre et al.'s (2009) study. Those taxa for which these authors 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 in the Fabre et al. study: see above) are indicated as "NA" (nonapplicable) in Figure 1 (N.B., the approximate time of origin of the genus *Homo*, 2.4 MY, follows Wood and Lonergan 2008). The primate specimens were obtained from the following institutions: the Primate Foundation of Arizona (PFA), the Department of Anatomy (GWUANA) and the Department of Anthropology (GWUANT) of the George Washington University, the Department of Anatomy of Howard University (HU), the Department of Anatomy of Valladolid University (VU), the Cincinnati Museum of Natural History (CMNH), the San Diego Zoo (SDZ), and the Canadian Museum of Nature (CMN). For each taxon, we provide the Linnean binomial, its source, its unique identifier, the number of specimens from that source, and the state of the specimens (alc. = alcohol fixed; fre. = fresh; for. = formalin embalmed). Apart from the primates dissected for this study, we have dissected specimens from all the major groups of vertebrates; a list of the dissected nonprimate vertebrate specimens is given in Diogo and Abdala (2010).

Primate specimens dissected. *Aotus nancymae* GWUANT AN1, 1 (fre.; adult female). *Callithrix jacchus* GWUANT CJ1, 1 (fre.; adult male). *Cercopithecus diana* GWUANT CD1, 1 (fre.; adult female). *Colobus guereza* GWUANT CG1, 1 (fre.; adult male). *Gorilla gorilla*: CMS GG1, 1 (fre.; adult male); VU GG1, 1 (fre.; adult female). *Homo sapiens*: GWUANA HS1–16, 16 (for.). *Hylobates gabriellae*: VU HG1, 1 (fre.; infant male). *Hylobates lar*: HU HL1, 1 (for.; adult male). *Lemur catta*: GWUANT LC1, 1 (fre.; adult male). *Loris tardigradus*: SDZ LT53090, 1 (fre.; adult male). *Macaca fascicularis*: VU MF1, 1 (fre.; adult male). *Macaca mulatta*: HU MM1, 1 (for.; adult male). *Macaca silenus*: VU MS1, 1 (fre.; adult male). *Nycticebus coucang*: SDZ NC41235, 1 (fre.; adult female); SDZ NC43129, 1 (fre.; adult female). *Nycticebus pygmaeus*: VU NP1, 1 (fre.; adult female); VU NP2, 1 (fre.; adult male); SDZ NP40684, 1 (fre.; adult female); SDZ NP51791, 1 (fre.; adult female). *Pan troglodytes*: PFA 1016, 1 (fre.; adult female); PFA 1009, 1 (fre.; adult female); PFA 1051,

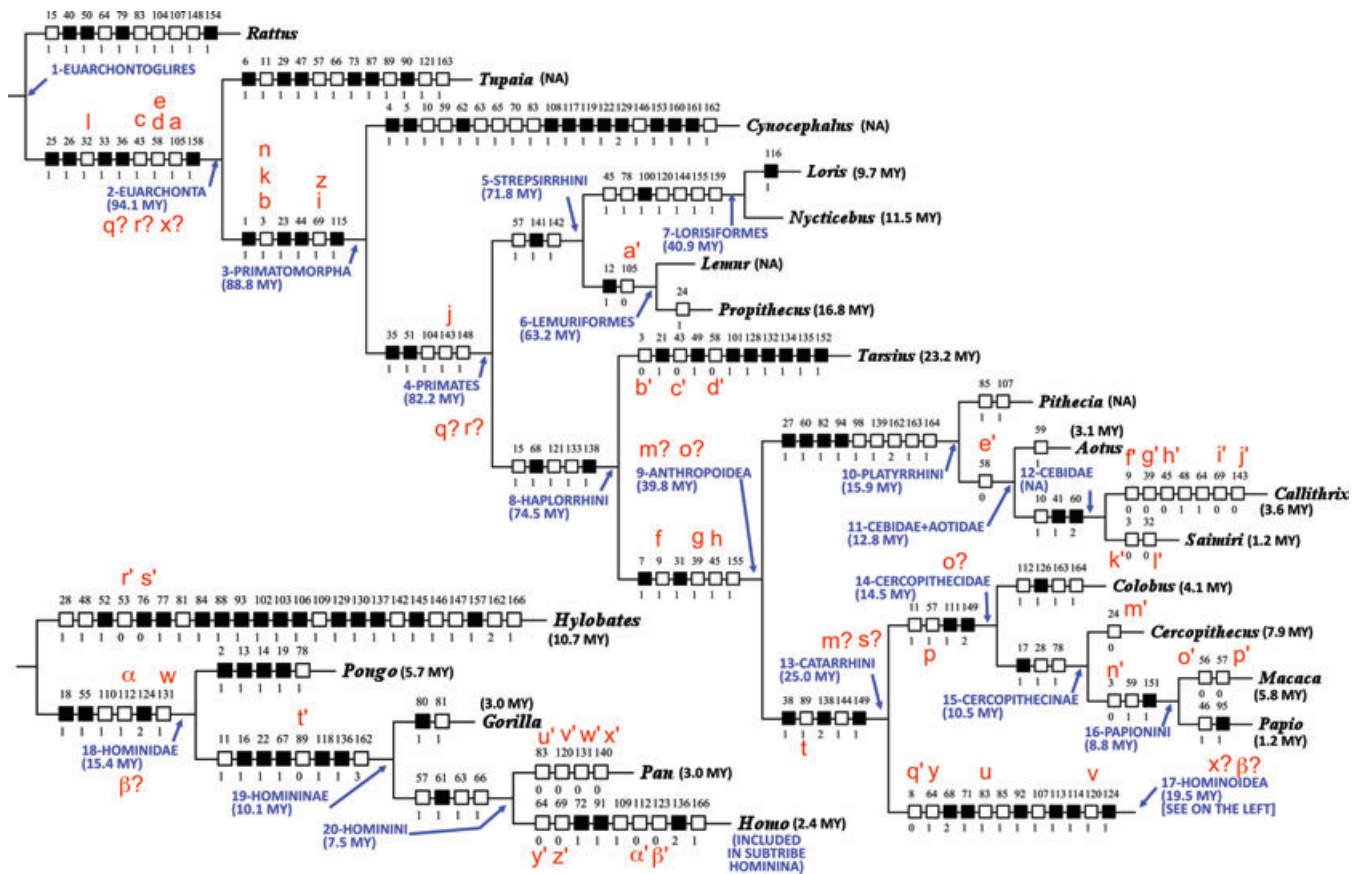


Figure 1. Single most parsimonious tree (L 301, CI 58, RI 73) obtained from the analysis of 166 characters of the head, neck, pectoral, and forelimb musculature (Diogo and Wood, 2011, 2012; see Appendix). The unambiguous transitions that occurred in each branch are shown in white (homoplastic transitions) and black (nonhomoplastic transitions) squares (numbers above and below the squares indicate the character and character state, respectively). Together with the name of each euarchontan clade is shown the respective estimate molecular divergence time, excepting for the genus *Homo* for which it is shown a time of origin exclusively based on the fossil record (see text for more 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).

1 (fre.; infant female); PFA 1077, 1 (fre.; infant female); PFA UNC (uncatalogued), 1 (fre.; infant male); HU PT1, 1 (for.; infant male); GWUANT PT1, 1 (for.; adult female); GWUANT PT2, 1 (for.; adult female); VU PT1, 1 (fre.; adult male). *Papio anubis* GWUANT PA1, 1 (fre.; adult female). *Pithecia pithecia*: VU PP1, 1 (fre.; adult male); GWUANT PP1, 1 (fre.; adult female). *Pongo pygmaeus*: HU PP1, 1 (for.; neonate male); GWUANT PP1, 1 (for.; adult male). *Propithecus verreauxi*: GWUANT PV1, 1 (fre.; adult female); GWUANT PV2, 1 (fre.; infant female). *Saimiri sciureus* GWUANT SC1, 1 (fre.; adult female). *Tarsius syrichta* CMNH M-3135, 1 (alc.; adult female).

Results

The phylogenetic reversions in the euarchontan clade suggested by the results of our comparative and phylogenetic analyses are indicated in Figure 1. A list of the 166 characters used in our

cladistic analyses is given in the Appendix. Details of the synapomorphies/apomorphies implied in our phylogenetic analyses are given in Diogo and Wood (2011); detailed tables describing, and photographs showing, each muscle of each of the primate taxa included in the tree of Figure 1 are given in Diogo and Wood (2012).

The most parsimonious tree obtained from the cladistic analysis of the 166 muscle-based characters from the head, neck, pectoral region, and upper limb examined by us (consistency index [CI] 58, retention index [RI] 73) has a total length of 301 steps, of which 220 are unambiguously optimized in the tree (squares in Fig. 1). Of these 220 evolutionary transitions, 28 (i.e., ca. 13%) are reversions to a plesiomorphic state. Taking into account the total number of characters (166) and the number of muscles (129) represented by the data in the cladistic analysis, there are ca. 0.17 unambiguous evolutionary reversions per character and ca. 0.21 unambiguous evolutionary reversions per muscle studied. Interestingly, when parsimony cladistic analyses of the head and neck

dataset (chars. 1–67) and of the pectoral and upper limb dataset (chars. 68–166; see Diogo and Wood, 2011) are performed separately, the frequency of reversions within the tree obtained from the former dataset (i.e., 18%, with a ratio of 0.30 reversions per muscle studied) is twice that within the tree obtained from the latter dataset (i.e., 9%, with a ratio of 0.16 reversions per muscle). That is, during the evolutionary history of primates there were more anatomical reversions among the head and neck musculature than among the pectoral and upper limb musculature.

The 28 unambiguous reversions to a plesiomorphic state are shown in Figure 1 (letters/symbols without a prime indicate the nodes where the respective original transitions from the plesiomorphic state to the derived state took place), and are summarized in Table 1. This table illustrates and complements what was stated in the paragraph above. This is because only 67 of the total 166 characters used in the cladistic analysis refer to head and neck muscles and, still, 16 of the 28 reversions listed in the table concern these muscles, that is, a mean of 0.23 reversions per each head and neck character. In contrast, 99 characters used in the cladistic analysis refer to pectoral and upper limb muscles, and only 12 reversions listed in the table concern these latter muscles, that is, a mean of 0.12 reversions per each pectoral and upper limb character.

Discussion

The results described above and illustrated in the tree of Figure 1 suggest that at least with respect to the musculature of the head and neck, pectoral region and the upper limb evolutionary reversions played a substantial role in primate and human evolution. One in seven of the 220 evolutionary transitions that are unambiguously optimized in this tree are reversions to a plesiomorphic state ($N = 28$). Of the 28 reversions shown in this tree, six played a direct role in our own evolution, that is, they occurred in the nodes that lead to the origin of modern humans (Fig. 1). One occurred at the node leading to the Hominoidea (q' : reversion of “Temporalis has a pars suprazygomatica”), one at the node leading to the Homininae (t' : reversion of “Latissimus dorsi and teres major are fused”), and four reversions occurred within the subtribe Hominina (y' , z' , α' , and β' : reversions of “Anterior portion of sternothyroideus extends anteriorly to the posterior portion of the thyrohyoideus,” of “Rhomboideus major and rhomboideus minor are not distinct muscles,” of “Tendon of flexor digitorum profundus to digit 1 is vestigial or absent,” and of “Flexor carpi radialis originates from the radius”; NB, the genus *Pan* is included in the other Hominini subtribe, the Panina).

One of the reversions that occurred within the subtribe Hominina, z' , violates Dollo’s law (i.e., a structure that was phylogenetically lost was later reacquired). That is, both the rhomboideus major and rhomboideus minor are plesiomorphically present in

Euarchontoglires and then at the node leading to the last common ancestor (LCA) of dermopterans and primates (ca. 88.8 MY: Fig. 1) the two muscles became fused, but they are again present as separate muscles in *Homo* (ca. 2.4 MY: Fig. 1; Table 2). This case is thus similar to the striking example reported by Wiens (2011) concerning the loss of mandibular teeth in the ancestor of modern frogs and their reappearance in the frog genus *Gastrotheca* (see above). This is because the alternate hypothesis, that is, that the rhomboideus minor was lost independently in all the Primatomorpha taxa that do not have this muscle, is cladistically very unlikely (i.e., three steps against the 10 steps required for independent losses in dermopterans, strepsirrhines, tarsiers, *Pithecia*, *Aotus*, *Saimiri*, hylobatids, orangutans, gorillas, and chimpanzees). It should be noted that *Callithrix* and the Cercopithecinae usually have a rhomboideus major and a rhomboideus minor but it is not clear if the Colobinae usually have both these muscles. Therefore, it is not clear if the rhomboideus minor became a distinct muscle in the subfamily Cercopithecinae or instead in the family Cercopithecidae—which includes both the Cercopithecinae and the Colobinae; that is why only three steps are unambiguously optimized in the tree: loss in Primatomorpha and reacquisition in *Homo* and *Callithrix*.

Eight other reversions within the tree shown in Figure 1 also violate Dollo’s law. The approximate time frame over which each of these reversions occurred is indicated in Table 2. Some of the alternate hypotheses (i.e., no violation of Dollo’s law) for most of these cases are as unlikely as is the alternate hypothesis stated above (see Table 2). The eight cases include: (a') reversion of “Biceps brachii has no bicipital aponeurosis” (apart from *Lemur* and *Loris* within the euarchontan taxa examined the aponeurosis is also usually present in hominoids except *Pongo*, so it is not clear if hominoids reacquired the aponeurosis and it was subsequently lost again in *Pongo*, or if was reacquired independently in the Hylobatidae and the Homininae); (c') reversion of “Spinotrapezius is not a distinct muscle”; (i') reversion of “Rhomboideus major and rhomboideus minor are not distinct muscles” in *Callithrix* (see above); (m') reversion 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 *Cercopithecus* or was lost in *Pithecia* and catarrhines and then reappeared in *Cercopithecus*); (r') reversion of “Pterygopharyngeus is not a distinct muscle” (either the derived condition was acquired in Euarchonta and then reverted in *Cynocephalus* and *Hylobates* or it was acquired in *Tupaia* and primates and then reverted in *Hylobates*); (v') reversion of “Epirochleoanconeus is not a distinct muscle”; (w') reversion of “Contraheentes digitorum are missing”; (x') reversion of “Flexores breves profundi are fused with the intermetacarpales, forming the dorsal interossei” (either the derived condition was acquired in *Tupaia*, in *Cynocephalus*, in platyrrhines, and in hominoids and then reverted in *Pan* or it

Table 1. List of the 28 reversions shown in Figure 1 (Anat. region, anatomical region; Ch. state ch., character state change; Rev., reversion). For more details, see text and Appendix.

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 "Cricoarytenoideus 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 probably arose in catarrhines or in other more inclusive clade and then was uniquely reverted in <i>Hylobates</i> , but see notes in text)	[76:1→0]	Pectoral
(t') Rev. 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 "Contraheutes digitorum are missing"	[131:1→0]	Hand
(x') Rev. of "Flexores breves profundi are fused with the intermetacarpales, forming the dorsal interossei" (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

Table 2. Time frame over which lost traits were regained within the euarchontan clade according to our phylogenetic study and using the estimate times provided by Fabre et al. (2009): N.B., the approximate time of origin of the genus *Homo*, 2.4 MY, follows Wood and Lonergan (2008). For more details, see text.

Structure that was regained, violating Dollo's law (letters shown before the description of each structure correspond to letters shown in Figure 1)	Number of evolutionary steps according to the hypothesis that violates Dollo's law (in bold) versus number of evolutionary steps that one would need to assume in order to not violate Dollo's law (in nonbold, 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 brachial artery and the median nerve running underneath)	2 vs 4 (loss in <i>Tupaia</i> , <i>Cynocephalus</i> , loriforms, and haplorhines)	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 vs 4 (loss in <i>Tupaia</i> , <i>Cynocephalus</i> , strepsirrhines, and anthropoids)	94.1 MY	23.2 MY	70.9 MY
(f') 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 vs 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 vs 4 (loss in <i>Pithecia</i> , <i>Colobus</i> , Papiomini, 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 corresponds 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 vs 6 (loss in <i>Tupaia</i> , strepsirrhines, tarsiers, platyrrhines, cercopithecoidea, and hominoidea)	94.1 MY or 82.2 MY	10.7 MY	83.4 MY or 71.5 MY (mean = 77.4 MY)
(v') Epitrochleoaneoneus (N.B., the epitrochleoaneoneus 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 vs 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 vs 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 vs 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 vs 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

was acquired in Euarchonta and then reverted in strepsirrhines, in *Tarsius*, in cercopithecids, and in *Pan*).

As the development of the muscular system is a complex process that involves, on the one hand, the fusion and/or reabsorption of elements and, on the other hand, the splitting and/or the neomorphic origin of elements (see, e.g., Diogo and Abdala, 2010), one would think that this system is particularly prone to the occurrence of evolutionary reversions leading to either a decrease or an increase of the total number of muscles of the descendant taxa. As can be seen in Table 2, the average time between a structure's loss and reacquisition was ca. 50.9 MY. In the nine cases summarized by Wiens (2011; his Table 2 plus his *Gastrotheca* example), the mean for the time between loss and reacquisition was ca. 72.8 MY ($[(25 + 32) / 2]$, for the reappearance of a larval stage in plethodontid salamanders) + [40, for the reappearance of a larval stage in hemiphractid frogs + $[(95 + 120) / 2]$, for the reappearance of digits in amphisbaenian lizards of the genus *Bipes*] + $[(20 + 60) / 2]$, for the reappearance of digits in gymnophthalmid lizards of the genus *Tretioscincus*] + [15, for the reappearance of digits in gymnophthalmid lizards of the genus *Bachia*] + $[(20 + 35) / 2]$, for the reappearance of digits in scincid lizards of the genus *Scelotes*] + $[(30 + 80) / 2]$, for the reappearance of eggshell in the boid snake *Eryx*] + $[(41 + 79) / 2]$, for the reappearance of shell coiling in snails] + $[(225 + 338) / 2]$, for the reappearance of mandibular teeth in the frog genus *Gastrotheca*]/9). But if the remarkable *Gastrotheca* example is excluded the mean would be ca. 46.7 MY, so it would be actually similar to the mean obtained in our study, indicating that in reality muscles are not more prone to evolutionary reversions than are external or hard tissue structures; this would be in line with the results of recent myology-based cladistic analyses of teleostean and of bony fish higher level phylogeny, which pointed out that muscles are in general less prone to homoplasy than are skeletal structures (for a review, see Diogo and Abdala, 2010). As noted by Wiens (2011), the temporal data reported by him, and also reported in the present study (Table 2), clearly contradicts explanations that defend the validity of Dollo's law. For example, according to Marshall et al. (1994), structures lost after more than 10 MY can almost never be regained because genes and developmental pathways that are not maintained by selection will decay due to mutational changes. But in all of the 18 case studies reported by us and surveyed by Wiens (2011), more than 10 MY had elapsed between a structure's loss and its reacquisition.

One of the flaws of Marshall et al.'s (1994) explanation is that the phylogenetic loss of structures is not always related to a complete loss of the developmental pathways. As noted by Wiens (2011), recent studies suggest that most of the developmental pathways for tooth development are maintained in at least some birds (e.g., chicken) despite the absence of teeth in adult birds for more than 60 MY. Our comparative analyses provide strong evidence to

support the idea that the reacquisition of anatomical structures that were missing for long periods of time in adults of a certain clade may be often related to cases where the developmental pathways to form these structures were actually maintained in the members of that clade (N.B., it should be noted that many developmental pathways function in the formation of multiple anatomical structures, thus selection may maintain them for forming these other structures: e.g., Gould 1977, 2002; see below). An illustrative example of this concerns the presence/absence of the contrahentes digitorum in adult hominids. As explained above, chimpanzees display a reversion of a synapomorphy of the Hominidae (acquired at least 15.4 MY ago: Fig. 1; Table 2) in which adult individuals have two contrahentes digitorum (in adults of other hominid taxa there is usually none) other than the adductor pollicis, one going to digit 4 and the other to digit 5. According to Marshall's (1994) theory, after 15.4 MY of evolution, the genes and developmental pathways needed to form the contrahentes should no longer be maintained by selection. However, detailed studies of the development of the hand muscles (e.g., Cihak, 1972) have shown that karyotypically normal modern human embryos *do have* contrahentes going to various fingers and that these muscles are lost during later embryonic development (Fig. 2A). Moreover, other studies (e.g., Dunlap et al., 1986) have shown that in karyotypically abnormal modern humans such as individuals with trisomies 13, 18, or 21, the contrahentes often persist until well after birth (Fig. 2B). 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 intermetacarpales in adult chimpanzees (Fig. 1, Table 2) is probably also related to paedomorphic events because Cihak (1972) also showed that the intermetacarpales *are also present* as distinct muscles in early embryos of karyotypically normal modern humans.

According to some authors, cases where complex structures are formed early in ontogeny just to become lost/indistinct in later developmental stages (the so-called "hidden variation") may allow organisms to have a great ontogenetic potential early in development, that is if there are for instance external perturbations (i.e., change in the environment, e.g., climate change, environment occupied by new species, etc.) evolution can use that potential (adaptive plasticity) (e.g., West-Eberhard 2003). However, authors such as Gould (1977) and Alberch (1989) have suggested that the occurrence of examples such as those cited above argue in favor of a "constrained" rather than an "adaptationist" view of evolution. This is in line with the view defended by the authors of more recent studies such as Galis and Metz (2007, pp. 415–416), who stated that "without denying the evolutionary importance of phenotypic plasticity and genetic assimilation, we think that for the generation of macroevolutionary novelties the evidence

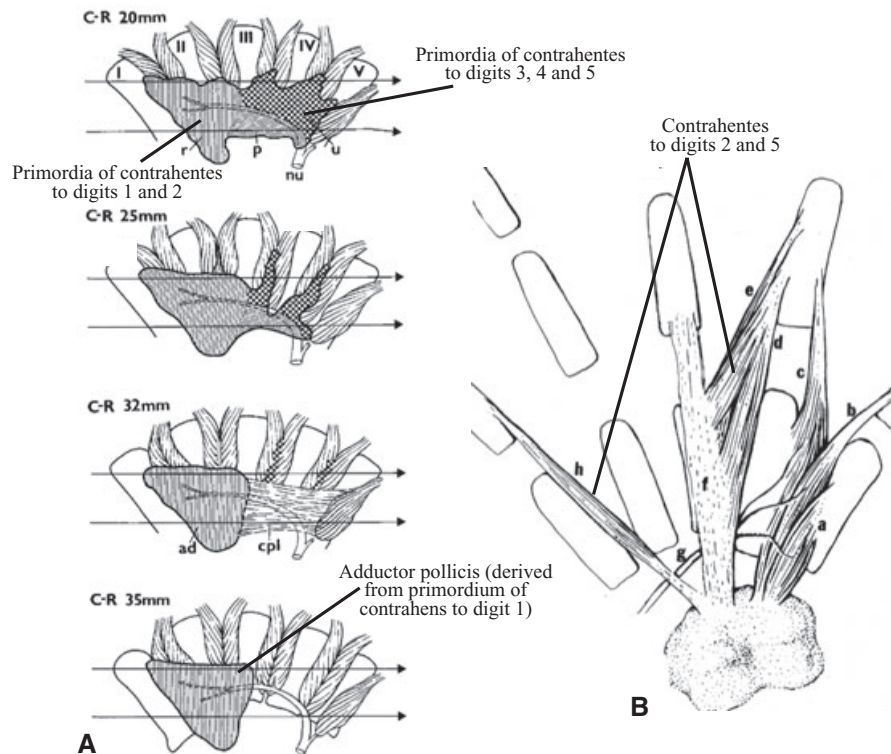


Figure 2. (A) Ontogeny of the contrahentes digitorum in the hand of a karyotypically normal human embryos showing how the contrahentes to digits other than digit 1 are usually lost (reabsorbed) early in development (modified from Cihak, 1972). Part of the interossei primordia (i.e., the flexores breves profundi layer) is shown between the metacarpals. r, u, p = radial, proximal, and ulnar parts of contrahentes layer; nu = ulnar nerve; ad = adductor pollicis; cpl = contrahens plate; I-V = metacarpals I-V; CR = crown-rump length of the embryos. (B) Deep left hand musculature of a trisomy 18 neonate (100-days old, female) showing the presence of contrahentes to digits 2 and 5 (the more superficial muscles, as well as the adductor pollicis, are now shown; modified from Dunlap et al., 1986). a, opponens pollicis; b, "interosseous palmaris of Henle"; c, interosseous dorsalis 1; d, contrahens to digit 2; e, interosseous palmaris 1; f, contrahens fascia/medial raphe; g, deep branch of ulnar nerve; h, contrahens to digit 5.

for the impact of hidden variation is, thus, far limited." We are inclined to agree that hidden variation may have a limited role for the generation of *new* evolutionary novelties. However, we would like to add that, as explained above, hidden variation may have a much more relevant role for the *reappearance* of some traits associated with these novelties, that is, for the occurrence of anatomical reversions violating Dollo's law.

In *Ontogeny and Phylogeny*, Gould argues that although Haeckel's hypothesis that the ontogeny of one organism recapitulates the adult stages of its ancestors (i.e., recapitulation) has been refuted, researchers often use this idea as a "straw-man" to deny that there is often a parallel between ontogeny and phylogeny. According to Gould such a parallel exists and is probably driven more by phylogenetic/ontogenetic constraints than by adaptive plasticity. The examples of the contrahentes and of the intermetacarpales support Gould's arguments in the sense that in these two case studies there is a parallel between ontogeny and phylogeny. That is, in "normal" modern human ontogeny the muscles are evident

and then became lost or indistinct later in ontogeny; during the recent evolutionary history of modern humans the muscles were plesiomorphically present and then became lost. This is not recapitulation in the Haeckelian sense: the contrahentes digitorum and the intermetacarpales of karyotypically "normal" 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. That is, the developmental pathways that result in the presence of these muscles in the adults of the latter taxa have not been completely lost in modern humans, even after several millions of years, probably because these pathways are related to those involved in the development of other structures that *are* present and functional in modern humans adults. That is, these developmental pathways are probably maintained in modern humans because of ontogenetic constraints. Regarding the occurrence of the evolutionary reversions that resulted in the presence of the contrahentes and of distinct intermetacarpales in extant chimpanzees, this might

either be the result of adaptive evolution or instead a by-product of pedomorphic events related to other structural adaptations. For instance, it is intuitively unlikely that the persistence of contrahentes in the later ontogenetic stages of karyotypically abnormal modern humans such as individuals with trisomies 21, and particularly 13 and 18 (which usually die before or soon after birth) is the result of adaptive evolution and natural selection. What seems to be clear is that the presence of distinct contrahentes digitorum and intermetacarpales in adult chimpanzees is very likely due to a prolonged or delayed development of the hand musculature of these apes, that is, in this particular case extant chimpanzees are seemingly more neotenic than modern humans. This is in line with other recent studies that have pointed out that, although in the literature it is often stated that modern humans are in general more neotenic than other primates, both pedomorphic and peramorphic processes have actually been involved in the mosaic evolution of humans and of other hominoids (see, e.g., Bufill 2011, and references therein).

In summary, the present study provides evidence that at least with respect to the musculature of the head and neck, pectoral region and the upper limb evolutionary reversions played a substantial role in primate and human evolution. Some of these reversions clearly violate Dollo's law and at least two of these violations probably involve the maintenance of ancestral developmental pathways (i.e., cases w' and x' in Table 2 and Fig. 1). Further detailed developmental studies of the muscles of modern humans and of other primates are needed to further investigate the other seven examples reported in Table 2 to determine whether there is evidence that these may also involve the maintenance of plesiomorphic ontogenetic pathways during long periods of trait absence. In addition, more studies are needed to analyze the occurrence, frequency, and temporal information of reversions within the evolutionary history of other primate soft as well as hard structures and to determine if those reversions violate, or do not violate, Dollo's law.

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Supporting Information

Supporting Information may be found in the online version of this article.

Appendix S1: List of the 166 Characters included in the Cladistic Analyses.

Supporting Information may be found in the online version of this article.

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[Correction added after online publication July 24, 2012: The appendix was removed from this article and is now available online as Supporting Information.]