Evolution and homologies of primate and modern human hand and forearm muscles, with notes on thumb movements and tool use

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A B S T R A C T

In this paper, we explore how the results of a primate-wide higher-level phylogenetic analysis of muscle characters can improve our understanding of the evolution and homologies of the forearm and hand muscles of modern humans. Contrary to what is often suggested in the literature, none of the forearm and hand muscle structures usually present in modern humans are autopomorphic. All are found in one or more extant non-human primate taxa. What is unique is the particular combination of muscles. However, more muscles go to the thumb in modern humans than in almost all other primates, reinforcing the hypothesis that focal thumb movements probably played an important role in human evolution. What makes the modern human thumb myology special within the primate clade is not so much its intrinsic musculature but two extrinsic muscles, extensor pollicis brevis and flexor pollicis longus, that are otherwise only found in hylobatids. It is likely that these two forearm muscles play different functional roles in hylobatids and modern humans. In the former, the thumb is separated from elongated digits by a deep cleft and there is no pulp-to-pulp opposition, whereas modern humans exhibit powerful thumb flexion and greater manipulative abilities, such as those involved in the manufacture and use of tools. The functional and evolutionary significance of a third peculiar structure, the intrinsic hand structure that is often called the ‘interosseous volaris primus of Henle’ (and which we suggest is referred to as the musculus adductor pollicis accessorius) is still obscure. The presence of distinct contrahentes digitorum and intermetacarpales in adult chimpanzees is likely the result of prolonged or delayed development of the hand musculature of these apes. In relation to these structures, extant chimpanzees are more neotenic than modern humans.

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Introduction

An understanding of comparative myology is crucial for developing hypotheses about the functional morphology of the modern human forearm and hand, and particularly their involvement in the manufacture and use of tools (e.g., Day and Napier, 1961, 1963; Napier, 1962; Tuttle, 1969; Lewis, 1989; Marzke, 1992, 1997; Susman, 1994, 1998; Marzke et al., 1998; Susman et al., 1999; Tocheri et al., 2008). The relatively few publications that have included myological information in discussions of the evolution of the primate and modern human forearm and hand can be divided into two groups. Publications prior to the 1950s were mainly the work of comparative vertebrate, tetrapod or mammalian anatomists who, with the exception of authors such as Howell and Straus (1932) and Straus (1941a, b), usually investigated a wide range of non-primate species but only a few primate taxa (e.g., Brooks, 1886; Parsons, 1898; McMurrich, 1903a, b; Forster, 1917; Howell, 1936a, b; Haines, 1939, 1946, 1950; Straus, 1942a, b). This pattern contrasts with most of the reports published since the 1950s that have mainly focused on primates, or even more narrowly, on hominoids or on modern humans (Hominina: see Fig. 1), and when they did provide a non-primate comparative context it was a relatively narrow one (e.g., Abramowitz, 1955; Day and Napier, 1963; Dylevsky, 1967; Tuttle, 1969; Dunlap et al., 1985; Aziz and Dunlap, 1986; Susman, 1994, 1998; Marzke et al., 1998; Susman et al., 1999). A notable exception is Lewis’ (1989) book that includes detailed information based on his own dissections of a wide range of non-primate tetrapods.

These studies have generated hypotheses regarding the evolution of primate forearm and hand anatomy, among them that modern humans are derived relative to other extant primates in possessing a true flexor pollicis longus, a deep head of flexor pollicis...
nomenclature of the forearm and hand muscles of primate and non-primate tetrapod taxa has been the subject of some confusion and controversy (see Diogo, 2007, 2009; Diogo and Abdala, 2007, 2010; Diogo et al., 2009; Diogo and Wood, 2011, 2012). For example, statements that some non-hominoid primates have a separate flexor pollicis longus (e.g., Marzke, 1997; Shrewsbury et al., 2003) refer to older publications that often used the name ‘flexor pollicis longus’ for the tendon of the flexor digitorum profundus that inserts onto digit 1 and not for a separate flexor pollicis longus that has a distinct belly and tendon (see below).

In recent papers (Diogo and Abdala, 2007; Diogo et al., 2009; Abdala and Diogo, 2010; Diogo and Wood, 2011) and monographs (Diogo, 2007; Diogo and Abdala, 2010; Diogo and Wood, 2012), Diogo and colleagues have reported the results of their long-term dissection-based study of the comparative anatomy, homologies and evolution of the pectoral and forearm muscles of all major groups of non-primate vertebrates and representatives of all of the major primate higher taxa. Diogo and Wood (2011, 2012) combined data from these 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 (Fig. 1) and for a range of outgroups (tree-shrews, dermopterans and rodents). A goal of the project was to establish the homologies of the pectoral and forelimb muscles of vertebrates and to provide the comparative context for more detailed evolutionary and taxon-based analyses.

The present paper uses data from these dissections to test hypotheses about the evolution of the hand myology of modern humans. Because we have dissected members of all of the major primate groups and the major non-primate vertebrate taxa, we can better understand the descriptions of authors that use different nomenclatures for these muscles. This has allowed us to clarify much of the nomenclatural confusion involved in the descriptions of the forearm and hand muscles of primates (see above). We also use these data to critically examine the proposition that modern humans are derived in having a flexor pollicis longus, deep head of flexor pollicis brevis, a ‘volar interosseous’ or ‘interosseous volaris primus’ of Henle, and an extensor pollicis brevis.

Materials and methods

We dissected representatives of each major extant non-hominoid primate clade (Strepsirrhini, Tarsiiformes, New World monkeys and Old World monkeys) and of each of the five major groups of living hominoids (i.e., hylobatids, orangutans, gorillas, chimpanzees, and modern humans) (Fig. 1). With a few exceptions, we use the same taxonomic nomenclature as Diogo and Wood (2011). Data included in the analysis come from four strepsirrhine genera, two from the infraorder Lemuriformes (Lemur, family Lemuridae; Propithecia, family Indriidae) and two from the infraorder Lorisiformes (Loris and Nycticebus, family Lorisidae); the single extant genus of the infraorder Tarsiiformes, Tarsius; representatives of three of the four extant platyrrhine families: Saimiri and Callithrix (Cebidae, subfamilies Saimiriinae and Callithrichinae, respectively), Pithecia (Pitheciidae), and Aotus (Aotidae; the other platyrrhine family being the Atelidae); the two extant subfamilies of Old World monkeys (family Cercopithecidae) represented by Colobus (Colobinae), Papio, Macaca and Cercopithecus (Cercopithecidae; the two former genera represent the tribe Papionini, while the latter genus represents the other extant tribe of the subfamily, the Cercopithecinae); and five extant hominoid genera: Hylobates (Hylobatidae), Pongo (Hominidae, Ponginae), Gorilla (Hominidae, Hominini, Gorillini), Pan (Hominidae, Hominina, Panini, Panina), and Homo (Hominidae, Homininae, Hominini, Hominina) (Fig. 1). We use the traditional classification that recognizes a single extant
hylobatid genus (*Hylobates*; including species such as *Hylobates syndactylus*, *Hylobates lar*, *Hylobates gabriellae* and *Hylobates hoolock*, among others: for more details see Diogo and Wood, 2011). Apart from the primates dissected for this study, we have dissected specimens from all of the major groups of vertebrates. A list of the dissected non-primate vertebrate specimens is given in Diogo and Abdala (2010).

The nomenclature for the forearm and hand muscles follows that of Diogo and Abdala (2010) (see Table 1). We addressed the problem of inconsistent usage of some specific taxonomic names in older systematic and anatomical studies, particularly those prior to Osman Hill’s studies in the 1950s (e.g., Hill, 1953, 1955, 1957, 1959, 1960, 1962, 1966, 1970, 1974; see References) by carefully reviewing all of the names and synonyms used in those studies (see Diogo and Wood, 2011). Discussions of the evolutionary changes occurring in each of the major primate branches are based on the phylogenetic results of Diogo and Wood (2011) (Fig. 1). The primate specimens were mainly dissected by RD, and 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. Regarding the sample size used in the cladistic study of Diogo and Wood (2011) and in the discussions of the present paper, two points should be stressed. First, it is difficult to find primate, and particularly ape, specimens in circumstances where careful dissection can take place. During this project, we made a considerable effort to establish connections with the major museums and zoos in the United States and beyond. This effort resulted in us being able to dissect, for example, two fresh gorillas, one fresh and one formalin embalmed Pongo, and six fresh and three formalin embalmed chimpanzees. The second point is that the sample size used in that cladistic study and in the discussions provided here refers to the specimens dissected by us and the total number of specimens reported in the numerous publications that were analysed in the extensive review of the literature undertaken by Diogo and Wood (2011) and particularly Diogo and Wood (2012). Thus, when we code and discuss each character we take into account all of the information available, and in numerous cases the total sample size is substantial when compared with cladistic studies of other animal species that were based on muscles (see, e.g., Diogo, 2007). For example, for character, 118 (the presence/absence of the palmaris longus) Diogo and Wood (2011) took into account information obtained from dissections of more than 20 hylotabts, 19 orangutan, 25 gorilla, and 39 chimpanzee specimens. For this character, the sample size just for apes was >103 specimens.

**Primate specimens dissected**

*Aotus nancymaeae*: GWUANT AN1, 1 (fresh; adult female). *Callitrichus jaccus*: GWUANT CJ1, 1 (fresh; adult male). *Cercocebus diana*: GWUANT CD1, 1 (fresh; adult female). *Colobus guereza*: GWUANT CG1, 1 (fresh; adult male). *Corilla gorilla*: CM5 CG1, 1 (fresh; adult male); VU GG1, 1 (fresh; adult female). *Homo sapiens*: GWUAN H51-16, 16 (formalin); HU D43, 1 (formalin); HU D45 (formalin). *Hylobates gabriellae*: VU HG1, 1 (fresh; infant male). *Hylobates lar*: HU HL1, 1 (formalin; adult male). *Lemur catta*: GWUANT LC1, 1 (fresh; adult male). *Loris tardigradus*: SDZ LT303050, 1 (fresh; adult male). *Macaca fascicularis*: VU MF1, 1 (fresh; adult male). *Macaca mulatta*: VU MMF, 1 (formalin; adult male).

*silenus*: VU MS1, 1 (fresh; adult male). *Nycticebus coucang*: SDZ NC41235, 1 (fresh; adult female); SDZ NC43129, 1 (fresh; adult female). *Nycticebus pygmaeus*: VU NP1, 1 (fresh; adult female); VU NP2, 1 (fresh; adult male); SDZ NP40684, 1 (fresh; adult female); SDZ NPS1791, 1 (fresh; adult female). *Pan troglodytes*: PFA 1016, 1 (fresh; adult female); PFA 10091, 1 (fresh; adult female); PFA 1051, 1 (fresh; infant female); PFA 1077, 1 (fresh; infant female); PFA UNC (uncatalogued), 1 (fresh; infant male); HU PT1, 1 (formalin; infant male); GWUANT PT1, 1 (formalin; adult female); GWUANT PT2, 1 (formalin; adult female); VU PT1, 1 (fresh; adult male). *Papio anubis*: GWUANT PA1, 1 (fresh; adult female). *Pithecus pithecus*: VU PP1, 1 (fresh; adult male); GWUANT PP1, 1 (fresh; adult female). *Pongo pygmaeus*: HU PP1, 1 (formalin; neonate male); GWUANT PP1, 1 (formalin; adult male). *Propithecus verreauxi*: GWUANT PV1, 1 (fresh; adult female); GWUANT PV2, 1 (fresh; infant male). *Saimiri sciureus*: GWUANT SC1, 1 (fresh; adult female). *Tarsius syrichta*: CMNH M-3135, 1 (alcohol; adult female).

**Results**

For each group of muscles (ventral forearm muscles, dorsal forearm muscles and intrinsic hand muscles), we discuss the results working from the more inclusive synapomorphic features (e.g., Primates, Haplorhini, Anthropoidea, etc.) to those apomorphies that are only found within *H. sapiens* (Fig. 1). Detailed tables that describe and use photographs to illustrate each muscle of each of the taxa included in the cladogram of Fig. 1 are included in Diogo and Wood (2012). Detailed descriptions of the phylogenetic characters used and of the synapomorphies obtained in our phylogenetic analyses are given there and in Diogo and Wood (2011).

**Ventral forearm musculature**

Among the synapomorphic features of the ventral forearm muscles, the most inclusive is the insertion of the flexor carpi radialis onto metacarpals II and III (e.g., Fig. 2), which was acquired in the Haplorhini (Fig. 1, feature 3). In most non-primate eutherian mammals, the flexor carpi radialis inserts onto metacarpal III (e.g., in rats), onto metacarpal II as is usually the case in *e.g., Lemur* and *Propithecus*, or, in a few cases (e.g., in flying lemurs), onto other structures, but it does not attach onto both metacarpals II and III, as it usually does in hylotabts (and in a few non-primate mammals, e.g., *Tupaias*). Two of the synapomorphies of hominoids concern the flexor digitorum superficialis. In non-hominoid primates, this muscle originates exclusively from the arm (medial epicondyle of humerus, common flexor tendon, and/or capsule of the elbow joint), but in hominoids the muscle usually also originates from the ulna and the radius (Fig. 1, features 10, 11). Another synapomorphy of hominoids is the loss of the epiprochleaconaceus, a small muscle that connects the medial epicondyle of the humerus to the olecranon process of the ulna. This muscle is usually present (presumably due to a secondary reversion) in chimpanzees (Fig. 1, feature 12). Pleiosomorphically in primates the pronator teres has a bony origin from the humerus only. In hylotabts, this muscle originates from the humerus and often, but not usually (i.e., <50% of the cases), from the ulna (Fig. 1, feature 13). In hominoids, the muscle originates from the humerus and usually (i.e., >50% of the cases) also from the ulna (Fig. 1, feature 16).

Pleiosomorphically, in primates the flexor digitorum profundus originates from the forearm (ulna, radius, and/or interosseous membrane) and arm (medial epicondyle and/or common flexor tendon). In hominoids (and also in Macaca as a homoplasy), this muscle does not originate from the medial epicondyle nor from the common flexor tendon (Fig. 1, feature 14). In our dissections, the flexor pollicis longus was present in modern humans and
The nomenclature of the muscles follows that of Diogo and Abdala (2010) and Diogo and Wood (2011, 2012). Data from evidence provided by our own dissections and comparisons and by a review of the literature. The black arrows indicate the hypotheses that are most strongly supported by the evidence available; the grey arrows indicate alternative hypotheses that are supported by some of the data, but overall they are not as strongly supported as are the hypotheses indicated by black arrows. APPEND. = appendicular; P = muscle present; VEN. = ventral; --- = muscle absent; access. = accessorius; dig. = digitorum; dor. = dorsales, flp. = flexores breves profundi; mi. = minimi; mus. = muscles; pal. = palmares; pre. = present in; prof. = profundus; ra. = radialis; int. = interossei.

Table 1

Scheme illustrating the authors' hypotheses regarding the homologies of the arm and hand muscles of adults of representative primate taxa; the flexor brevis profundus 2 (which corresponds to the 'deep head of the flexor pollicis brevis' of human anatomy) is listed here (and counted) as a distinct muscle, following the works done on numerous other mammals.

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hylobatids (Table 1, Fig. 1, feature 21; Figs. 2–4), confirming observations by previous researchers (e.g., Deniker, 1885; Hartmann, 1886; Kohlbrügge, 1890-1892; Hepburn, 1892; Keith, 1894b; Chapman, 1900; McMurrich, 1903a, b; Sonntag, 1924b; Howell, 1936a, b; Straus, 1942a; Jouflroy and Lessertisseur, 1960; Tuttle, 1969; Jouflroy, 1971; Van Horn, 1972; Lorenz, 1974; Marzke, 1992, 1997; Susman, 1994, 1998; Stout, 2000; Tocheri et al., 2008).

This is a potential example of parallelism in that from a similar ancestral configuration (i.e., the flexor digitorum profundus going to the distal phalanges of digits 1–5), there is an independent acquisition of a similar derived feature (differentiation of the belly of the flexor digitorum profundus going to digit 1, to form a separate flexor pollicis longus muscle). The belly of the flexor pollicis longus is distinct from the flexor digitorum profundus in all of the modern humans and the two hylobatids dissected by us (Fig. 2), but in the H. gabriellae (VU HG1) male infant there is a distal tendinous connection between the tendon of the former muscle and the tendon of the latter muscle that goes to digit 2 (Fig. 3). N.B., Fig. 2 shows some tissue that appears to run distally from the most lateral flexor digitorum profundus tendon to the flexor pollicis longus tendon just proximal to the wrist, but careful dissection established that there is no fleshy or tendinous connection between these two muscles in the photographed specimen. This connection reflects the ancestral, and probably embryonic, condition where these two muscles form a single structure (Diogo and Wood, 2011).

In the 18 modern humans dissected by us, we did not see as strong a tendinous distal connection between the two muscles as we found in the gibbon infant, but according to Lindburg and Comstock (1979) 31% of modern humans display some type of connection between these two muscles (see below). In the great apes, the tendon of the flexor digitorum profundus to digit 1 is often either a very thin, vestigial structure or it is absent (Fig. 5). According to the results of our cladistic analysis, it is more parsimonious to infer that this tendon became reduced in the last common ancestor (LCA) of hominids and became fully developed again in the Hominia (two steps) than to conclude that it became reduced independently in orangutans, gorillas and chimpanzees (three steps) (Fig. 1, features 15 and 21). However, in this case there are reasons to suggest that the cladistically less parsimonious hypothesis may be the most likely evolutionary hypothesis (see Discussion below).

Apart from the presence of a distinct flexor pollicis longus, modern humans also show a reversion of the character state ‘Flexor carpi radialis originates from the radius’ (Fig. 1, feature 23). Unlike the condition in modern humans (i.e., the only bony origin is from the medial epicondyle of the humerus), in great apes the flexor carpi radialis muscle also originates from the radius. However, it is not clear which is the usual condition for hylobatids, and, thus, whether a radial origin constitutes a synapomorphy of hominoids or of hominids. Hepburn (1892) and Kohlbrügge (1890-1892) noted a partial origin of flexor carpi radialis from the radius in various hylobatid species, as we did in our H. gabriellae and H. lar specimens, but other authors (e.g., Michelsen et al., 2009) have reported an exclusive origin from the humerus in species such as H. pileatus, H. moloch and H. syndactylus.
All of the non-Homininae (non-African ape and modern human) primates, as well as the non-primate mammals dissected by us, have a palmaris longus (e.g., Fig. 2). In gorillas, chimpanzees and modern humans, the palmaris longus is missing in at least 5% of the cases (Fig. 1, feature 18). The reviews of Keith (1899), Loth (1931), Sarmiento (1994) and Gibbs (1999) indicate that a palmaris longus is present in 64%, 15%, 36% and 31% of gorillas, respectively, and in 75%, 95%, 91% and 68% of chimpanzees, respectively, and more recent literature indicates that the muscle is present in 85% of modern humans (e.g., Gibbs, 1999; Gibbs et al., 2000, 2002).

**Dorsal forearm musculature**

With respect to the dorsal forearm muscles, an inclusive synapomorphy of anthropoids is the presence of both ulnar and humeral heads of the supinator (Fig. 1, feature 6). The plesiomorphic state in mammals (e.g., *Tupaia, Rattus* and *Cynocephalus*) and in primates (e.g., *Lemur, Propithecus* and *Tarsius*) is a single humeral head. Lorisiformes have independently acquired an ulnar head and thus they resemble anthropoids in that they have both humeral and ulnar heads. The other two forearm extensor apomorphies are much less inclusive. One, which characterizes the Homininae, is the exclusive insertion of the extensor indicis onto digit 2 (Fig. 1, feature 20). In other primates and in most other mammals, this muscle usually goes to more than one digit (e.g., Fig. 7; N.B., other authors use names such as ‘extensor indicis et tertius’ when the muscle goes e.g., to digits 2 and 3, but we follow the nomenclature of Diogo and Wood, 2012, who pointed out that the muscle should still be designated as extensor indicis in those cases in order to stress the homology of the muscle, whether it goes to a single digit or not). The other forearm extensor apomorphy, which characterizes the extant Hominina (and also the
Intrinsic hand musculature

Regarding the intrinsic hand muscles, inclusive synapomorphies include the presence of an opponens pollicis and an opponens digitii minimi (Table 1) that were acquired in the node leading to the Primates (Fig. 1, features 1, 2). The opponens pollicis became secondarily undifferentiated in a few primates (e.g., Callithrix) and one, or both, of these muscles may be present in some non-primate mammals such as rats. Strepsirrhines and most non-primate mammals have an undivided adductor pollicis. In the node leading to haplorrhines, this muscle became partly divided into transverse and oblique heads (Fig. 1, feature 5), and then in the node leading to catarrhines the muscle became further divided into well-separated transverse and oblique heads (Fig. 1, feature 7) (e.g., Figs. 4 and 5). Another synapomorphy of haplorrhines is the presence of more than two contrahentes digitorum (i.e., other than the adductor pollicis, which derive evolutionarily from the ancestral contrahens to digit 1; Table 1, Fig. 1, feature 4). The plesiomorphic condition for primates (e.g., Lemur, Propithecus, Loris and Nycticebus) as well as in non-primate taxa such as Rattus, Tupaiia and Cynocephalus, is to have only two contrahentes digitorum (usually to digits 2 and 5; Table 1). A synapomorphy of the Hominidae is the absence of contrahentes digitorum (Fig. 1, feature 17), but in the node leading to Pan there was a reversion to the plesiomorphic primate condition (i.e., adult chimpanzees usually have two contrahentes digitorum, but unlike in strepsirrhines these muscles usually go to digits 4 and 5; Table 1). N.B., the chimpanzees dissected by us have contrahentes, although in some cases the fleshy parts of these muscles were markedly reduced: for more details see, e.g., Diogo and Wood, 2012, in press). Another reversion that differentiates Pan from the other members of the Hominidae, as well as from hylobatids and New World monkeys is the presence of four intermetacarpals (i.e., the flexor brevis profundi and intermetacarpales do not fuse to form the dorsal interosseous) each connecting adjacent metacarpals (Table 1, Fig. 6; see Discussion below).

Apart from the presence of well-separated oblique and transverse heads of the adductor pollicis (see above) catarrhines are characterized by two synapomorphies. First, contrary to the plesiomorphic primate condition in which the opponens pollicis inserts onto the proximal and/or middle surfaces of the metacarpal I in catarrhines (and homoplascically also in the Lorisiformes) the opponens pollicis reaches the distal margin of this bone (Fig. 1, feature 8). Second, in catarrhines the opponens digitii minimi is divided into superficial and deep bundles, while in other primates and most other mammals this muscle is undivided (Fig. 1, feature 9).

According to our comparative and phylogenetic analyses, one of the synapomorphies of the Homininae (African great apes and modern humans) is that the ‘volar interosseus of Henle’ (or ‘interosseous volaris primus of Henle’), which very likely derives from...
a thin deep additional slip of the adductor pollicis (Diogo and Wood, 2011), is often (c. < 50% of cases) present (Fig. 1, feature 19), whereas in other primates and other mammals this muscle is nearly always, or always, absent. This synapomorphic Homininae condition where the muscle is often but not usually present (i.e., c. < 50% of cases) is seen in chimpanzees and gorillas (e.g., Fig. 5).

Modern humans display an autapomorphic condition within the Homininae because the muscle is found in most (≥50%) of the cases (see Table 1; Fig. 1, feature 24; Fig. 4).

Discussion

Four forearm and hand muscles (flexor pollicis longus, the so-called ‘deep head of the flexor pollicis brevis’, the so-called ‘volar interosseous of Henle’ and the extensor pollicis brevis) have been considered to be uniquely, or almost uniquely, found in modern humans. Below we provide a discussion of these structures and of the other forearm and hand structures to which they are anatomically and functionally associated, and consider their functional and evolutionarily significance in light of evidence from the fossil record and from biomechanical analyses.

Flexor pollicis longus

In modern humans, the flexor pollicis longus is innervated by the anterior interosseous nerve and it usually runs from the ventral surface of the radius and the interosseous membrane to the distal phalanx of the thumb. The different nomenclatures used to describe this muscle have resulted in some confusion. Day and Napier (1963) suggested that the flexor pollicis longus is present in Loris, Nycticebus, Tarsius, Aotus, Callicithrix, Saimiri, Macaca, Cercopithecus, Colobus, Papio and Homo, and this was the view that informed the cladistic studies of Groves (1986) and Shoshani et al. (1996). However, Day and Napier (1963) intended the term’s traditional usage (e.g., Barnard, 1875; Duckworth, 1904, 1915; Wood Jones, 1920; Sonntag, 1924a, b), which is to indicate the presence of a tendon of the flexor digitorum profundus to digit 1. They did not necessarily imply the presence of a distinct flexor pollicis longus muscle (i.e., separated from the flexor digitorum profundus, with a tendon exclusive to the thumb). In the Loris, Nycticebus and Tarsius specimens dissected by Burmeister (1846), Mivart and Murie (1865), Murie and Mivart (1872), Keith (1894a, b), Allen (1897), Woolard (1925), Miller (1943), Schultz (1984) and by us, the Aotus, Callicithrix and Saimiri specimens studied by Senft (1907), Beattie (1927), Hill (1957, 1960, 1962) and by us, the Macaca specimens examined by Haughton (1864, 1865), Howell and Straus (1932,
1933, Patterson (1942), Jacobi (1966), Kimura and Tazai (1970), Jouffroy (1971) and Landsmeer (1986) and by us, the Cercopithecus specimens investigated by Hill (1966) and Lewis (1989) and by us, the Colobus specimens dissected by Brooks (1886), Polak (1908), Jouffroy and Lessertisseur (1960) and by us, and the Papiro specimens studied by MacDowell (1910), Hill (1970), Swindler and Wood (1973), Tocheri et al. (2008) and by us there is no distinct flexor pollicis longus going exclusively to digit 1 (Table 1). Thus, the apparently contradictory statements in the literature about the presence/absence of a flexor pollicis longus in non-hominoid primates are mainly the result of nomenclatural pluralism and they should not be used as the basis of cladistic character states without additional clarification.

Our dissections confirm previous reports that in most non-hominoid primates the flexor digitorum profundus sends a tendon to digit 1. However, it is not independent of the tendons going to the other digits even though, when it is present, it flexes the distal phalanx of the thumb in the same way that the flexor pollicis longus does in modern humans. In the great apes, the flexor digitorum profundus tendon to digit 1 is usually either vestigial or even absent (e.g., Fig. 5). Strauss (1942b) showed, using evidence from both his own dissections and from data available to him in the literature, that among 47 chimpanzees such a tendon was absent in 14 individuals (30%), too small/thin to have had any useful function in 10.5 individuals (22%), and was in direct functional continuity with the radial muscle belly of the flexor digitorum profundus in 22 individuals (48%). Likewise, among 16 gorillas Strauss (1942b) showed that this tendon was absent in five individuals (31%), rudimentary in six individuals (41%), and present in four individuals (25%). Among 27 orangutans, the tendon was absent in 24 individuals (89%), rudimentary and functionless in two individuals (7%) and only completely developed in one individual (4%). Thus, there is no functioning tendon in c. 95% of orangutans, in c. 72% of gorillas and in c. 50% of chimpanzees.

In hylobatids, the anatomy of the flexor pollicis longus is more complex. Our de novo dissections (Table 1; Figs. 2–4) confirm that both modern humans and hylobatids have a flexor pollicis longus distinct from the flexor digitorum profundus, unlike the extensively-connected muscle bellies seen in other primates (corroborating the descriptions of authors such as Deniker, 1885; Hartmann, 1886; Kohlbrügge, 1890–1892; Hephburn, 1892; Keith, 1894b; Chapman, 1900; McMurrich, 1903a; b; Sonntag, 1924b; Howell, 1936a, b; Strauss, 1942a; Jouffroy and Lessertisseur, 1960; Tuttle, 1969; Jouffroy, 1971; Van Horn, 1972; Lorenz, 1974; Marzke, 1992, 1997; Susman, 1994, 1998; Stout, 2000; Tocheri et al., 2008). However, a few authors (e.g., Payne, 2001) suggest that in the Hylobates specimens dissected by them the flexor pollicis longus blends with, and is thus not really separate from, the flexor digitorum profundus.

In an influential paper about the evolution of tool use in the Hominina, Susman (1994: 1573, Fig. 3) stated that contrary to the condition in modern humans, chimpanzees and other primates have only a tendon that mimics the flexor pollicis longus and lacks a separate muscle belly; “in lesser apes (gibbons and siamangs) there is a muscle belly, but it is functionally coupled with the flexor digitorum profundus...electromyography experiments on an adult female gibbon (H. lar) did not elicit flexion of the thumb separate from flexion of the fingers, as is the case in humans”. The apparent inconsistency between Susman’s interpretation and the interpretations of researchers who have described the hylobatid flexor pollicis longus as distinct (e.g., Marzke, 1992) is likely due to the variable presence of a connective tissue ‘shunt’ (Tuttle, 1969) that connects the tendons of the flexor digitorum profundus and flexor pollicis longus (Tuttle (1969) referred to it as the ‘radial component of the flexor digitorum profundus musculature’) often at the level of the carpus in hylobatids. This shunt, which is commonly less substantial than the tendons it connects, is a slender flat (4–5 mm wide) structure that passes obliquely inferomedially from the tendon of the flexor pollicis longus to the lateral edge of the common flexor digitorum profundus tendons to digits 2–5. According to Tuttle, the ‘flexor shunt’ probably serves different functions during the various activities undertaken by hylobatids. For instance, he suggested that when the hand is used as an anatomical hook during vigorous arm-swinging, the ‘shunt’ probably transfers some of the contractile force of flexor pollicis longus to the flexor digitorum profundus tendons and thereby helps to stabilize the wrist. In contrast, when the hand is used for fine manipulation, particularly when the metacarpophalangeal joints of digits 2–5 are flexed, the ‘shunt’ is probably somewhat slack, allowing the flexor pollicis longus to independently flex the distal phalanx of the thumb. When the thumb is abducted to grasp large branches, the ‘shunt’ is probably also stretched to the extent that the distal phalanges of the thumb and the medial four digits are flexed synchronously to produce secure grips. As a result, and contrary to what occurs in Pan, Pongo and Gorilla, in hylobatids the pollex normally plays an active role in maintaining a suspended posture and in facilitating the distinctive locomotion of these hominoids. After observing living animals, Van Horn (1972) suggested that the flexor pollicis longus of hylobatids is important during the arm-pull phase of climbing, in which the terminal phalanx of the thumb is flexed as the animal lifts its weight from a previous support (i.e., this muscle is an important component of the power used to grasp). Stout (2000) found that the tendon of the flexor pollicis longus of hylobatids does not flex the distal phalanx of the thumb, but instead it adducts the thumb, flexes the pollical metacarpophalangeal joint and stabilizes the pollical interphalangeal joint. Further functional studies of hylobatids are needed to test these hypotheses, particularly because even among modern humans there is significant variation with respect to the presence of a fully independent flexor pollicis longus. For instance, as explained above according to an extensive review undertaken by Lindburg and Comstock (1979), only c. 70% of modern humans have a flexor pollicis longus that is anatomically entirely independent from the flexor digitorum profundus. Shrewsbury et al. (2003) posited that evidence of restrictive thumb/index tendosynovitis and pain in modern humans is usually associated with connections between the flexor pollicis longus and the flexor digitorum profundus. In some cases, the condition can be relieved by removing the connection between these muscles and occasionally the thickened flexor pollicis longus must be removed as well. According to Shrewsbury et al. (2003), the repetitive force used in a precision grip in concert with habitual repetitive behaviours associated with precision handling might have favoured independence of these two muscles as modern humans became increasingly dependent on the dexterity required to make and use tools.

There are reasons to consider that the tendon of the flexor digitorum profundus to digit 1 became independently reduced in orangutans, gorillas and chimpanzees, while the presence of a separate, robust flexor pollicis longus in hylobatids and modern humans may be associated with having a well-developed and/or functionally more independent thumb. The first hypothesis is supported by the fact that the tendon of the flexor digitorum profundus to digit 1 is highly variable in great apes. In a few cases it is fully developed, in others it is atrophied, in others it is ‘rudimentary’ and may no longer attach to the main body of the flexor digitorum profundus muscle, and in others it is completely missing (see above and also, e.g., Shrewsbury et al., 2003, Fig. 5). Strauss (1942b) included those cases where there is no continuity with the main body of the flexor digitorum profundus in the category of rudimentary, vestigial or functionless tendon to digit 1. However, it
is important to note that, as stressed by Shrewsbury et al. (2003), the tendon is not necessarily functionless in all of those cases. Within the specimens dissected by them, the tendon had an attachment pattern that was ligament-like in all four specimens of orangutan, two of the chimpanzees, and the two juvenile haram­dryas baboons. The tendon attached distally to the pollical distal phalanx and laterally to the radial and unlar basal tubercles. Tendon fibres in the haramdryas baboons had distal attachments to the ungual pul­per the distal phalangeal tuberosity. However, the proximal radial and unlar bands of the tendon both sent branches to the metacarpophalangeal joint in the region of the adductor pollicis insertion, and also (in the apes) in the region of the flexor pollicis brevis insertion. No fibres were found continuing fur­ther proximally over the wrist to the radial aspect of the flexor digitorum profundus tendon. According to Shrewsbury et al. (2003), this distal tethering of the tendon to digit 1 to bone on both sides of the distal interphalangeal joint probably helps to stabilize the joint.

The hypothesis that the presence of a separate, robust flexor pollicis longus in hylodonts and modern humans may be associated with having a well-developed and/or functionally more independent thumb is in line with the results of electromyography (Marzke et al., 1998) and hand pressure studies (Rolan et al., 2011; Williams et al., 2012) when various modern human subjects were manufacturing and using Oldowan tools as well as other objects. The recruitment of the flexor pollicis longus and the extensor pollicis brevis allowed the subjects to maintain the meta­carpophalangeal joint in extension (using the extensor pollicis brevis, which in modern humans usually attaches onto the proximal phalanx of the thumb: see below), while simultaneously using the flexor pollicis longus to flex the distal phalanx of the thumb at the pollical interphalangeal joint. The results from experiments documenting hand pressure during stone tool making underscore the importance of hand posture on the distribution of pressure across the thumb and other digits (Williams et al., 2012), supporting the suggestions of Marzke et al. (1998) suggestion that the differentiation of these two muscles needed to have occurred for early members of the human lineage to be able to habitually make effective stone tools.

Evidence from the fossil record also lends some support to the hypothesis that a well-developed tendon to digit 1, whether as part of flexor digitorum profundus or as a separate flexor pollicis longus, was the primitive condition for the Hominidea and probably the Pan-Homo LCA. Williams et al. (2003; Shrewsbury and Shrewsbury, 2006; Tocheri et al., 2008) have noted that the flexor pollicis longus (or flexor digitorum profundus to digit 1) does not insert onto the distal phalanx’s volar pit, or ‘proximal volar fossa’ (Shrewsbury et al., 2003), it is clear that the tendon inserts on the ridge that is, when present, just distal to the fossa (Susman, 1998; Shrewsbury et al., 2003). The presence of an attachment (ridge) to the distal pollical phalanx is seen in all of the fossil hominoid taxa known to date, including Proconsul (Bégun et al., 1994) and Ore­opithecus (Moyá-Solà et al., 1999). Similarly, all fossil pollical thumb distal phalanges attributed to (pre-modern) Homo show evidence of a volar ridge, with an accompanying proximal volar fossa (Shrewsbury et al., 2003) that marks the attachment of a tendon (Susman, 1998). The attachment site is also present on the distal pollical phalanges of both early and potential fossil taxa of the subtribe Hominina, including Orrorin tugenensis (Gommery and Senut, 2006; Almécija et al., 2010), Ardipithecus ramidus (Lovejoy et al., 2009), and Australopithecus afarensis (Ward et al., in press). Whether Orrorin is a member of the subtribe Hominina (Senut et al., 2001; Richmond and Jungers, 2008) or not (e.g., Wood and Harrison, 2011), the clear indication of a tendon insertion on the distal pollical phalanx at almost six million years ago suggests that either 1) the presence of tendon to digit 1 was present in the Pan-Homo LCA, is retained in the Hominina, and independently lost in the evolution of Pan and Gorilla (and possibly Pongo), or 2) that the Pan-Homo LCA lacked the tendon insertion, and that it evolved rapidly at the base of the Hominina clade independently of its evolution in hylodonts. In either scenario, the evolution of the flexor pollicis longus in hominoids involves homoplasy. In a recent paper, Almécija et al. (in press) strongly support the idea that the plesiomorphic hominoid, hominid and hominin condition is very likely a moderately long thumb, longer than the thumb of modern great apes, thus indirectly supporting the idea that the tendon of the flexor digitorum profundus to digit 1 became independently reduced in orangutans, gorillas and chimpanzees.

Some time between the late Pliocene and early Pleistocene, the thumb of the members of the subtribe Hominina evolved significantly greater robusticity, the thumb of modern humans being more robust than that of any other extant hominoids, including hyloba­tids (Susman, 1994). However, the hypothesis remains untested regarding whether other derived muscular features of the modern human hand occurred with the evolution of thumb robusticity.

Deep head of the flexor pollicis brevis and the ‘volar interosseous of Henle’

In modern humans, the so-called ‘deep head of the flexor pollicis brevis’ usually runs from the carpal region (e.g., capitate, occasionally from trapezoid) to the medial side of the palmar surface of proximal phalanx of digit 1 and/or an adjacent sesamoid bone (e.g., Fig. 4) and it is normally innervated by the deep branch of the ulnar nerve (and/or occasionally by the median nerve). The so-called ‘volar interosseous of Henle’ usually runs from the base of metacarpal 1 to the ‘wing tendon’ of the extensor apparatus of digit 1 (e.g., Susman et al., 1999). In the specimens examined by us, this latter structure, which is normally innervated by the deep branch of the ulnar nerve, may also originate from the carpal bones adjacent to metacarpal 1 and its insertion onto digit 1 may extend onto the proximal phalanx and/or sesamoid bone of the thumb (e.g., Fig. 4). Susman (1994; Fig. 3) suggested that the ‘deep head of the flexor pollicis brevis’ and the ‘interosseous volaris primus of Henle’ (as described above) are derived in modern humans. However, our comparative investigation suggests that the ‘deep head of the flexor pollicis brevis’ is present in most primates, while the volar interosseous of Henle is seen in <50% of a few primates including gorillas and chimpanzees (e.g., Fig. 5). Lewis (1989) embraced the hypothesis of Forster (1917) who suggested that the plesiomorphic condition for eutherian mammals is to have ten flexores breves profundi, each inserting onto the lateral and medial sides of each digit, and four intermetacarpales (see, e.g., Fig. 6) connecting the adjacent metacarpal bones. In primates, the plesiomorphic condition is the same, but two of the 14 muscles have differentiated, each forming two muscles: the flexor pollicis brevis and the opponens pollicis from flexor brevis profundus 1, and the flexor digiti minimi brevis and the opponens digiti minimi from flexor brevis profundus 10 (Fig 1, Table 1). In hominoids other than chimpanzees, as well as in New World monkeys, the flexores breves profundi 3, 5, 6 and 8 usually fuse with the intermetacarpales 1, 2, 3 and 4 to form the dorsal interossei 1, 2, 3 and 4, respectively, whereas the palmar interossei 1, 2 and 3 are derived directly from the flexores breves profundi 4, 7 and 9, respectively. The model of Lewis (1989), model, which explains why the dorsal interossei muscles are bipennate whereas the palmar interossei are unipennate, is supported by the developmental studies of authors such as Gihá (1972), which point out that at least some flexores breves profundi effectively become fused ontogenetically with the most dorsal intrinsic muscles of the hand (the intermetacarpales), forming the dorsal interosseous of adult modern humans. Chimpanzees have undergone a secondary
reversion to the plesiomorphic state, probably because their flexores breves profundi do not fuse with the intermetacarpals during ontogeny to form the dorsal interossei (Table 1; Fig. 6). As explained above, chimpanzees also display a secondary reversion of a synapomorphy of the Hominidae in that adult chimpanzees have two contrahentes digitorum in addition to the adductor pollicis, one going to digit 4 and the other to digit 5 (in other adult hominins there is usually none). Because the studies of Čihák (1972) suggest that in at least modern humans the contrahentes are lost (i.e., ‘reabsorbed’) during ontogeny, the presence of metacarpals and of contrahentes in chimpanzees is very likely due to a prolonged or delayed development of the hand musculature of these apes, i.e., in this particular case extant chimpanzees are seemingly more neotenic than modern humans (Diogo and Wood, in press). 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, the empirical data collected in the last decades reveal that both pedomorphic and peramorphic processes have been involved in the mosaic evolution of humans and of other hominoids (see, e.g., Buffet et al., 2011; and references therein).

The main controversy concerning the evolution and taxonomic distribution of the so-called ‘deep head of the flexor pollicis brevis’ and of the volar interosseous of H. enle mainly concerns the identity of one of the flexores breves profundi (i.e., number 2, which plesiomorphically in mammals goes to the ulnar side of digit 1). Although the so-called ‘volar interosseous of H. enle’ is usually not shown in modern human anatomical atlases, it is present in the majority of modern humans. For example, Abramowicz (1955), Lewis (1989), Susman et al. (1999), Henkel-Kopleck and Schmidt (2000) and Morrison and Hill (2011) report the presence of volar interosseous of H. enle in 100%, 92%, 86%, 69%, and 91%, respectively, of the individuals examined. This structure was also found in the 18 modern human individuals examined in this study (GWUANA HS1-6, HU D43 and HU D45; Fig. 4).

As the alternative name ‘interosseous volaris primus’ indicates, some authors consider that this structure, (e.g., Figs. 4 and 5; see below) corresponds to a vestigial flexor brevis profundus 2 (i.e., it is a fourth, and most radial, palmar interosseous). However, our comparative and phylogenetic analyses strongly suggest that the ‘interosseous volaris primus’ corresponds instead to a structure that is derived from a thin, deep additional slip of the adductor pollicis (Diogo and Wood, 2011) that we suggest should instead be named the adductor pollicis accessorius (see below and Table 1). In fact, the ‘interosseous volaris primus’ often blends with the adductor pollicis distally (see Diogo and Wood, 2011, 2012) and, at least in modern humans, it is innervated by the branches of the deep branch of the ulnar nerve that innervate the adductor pollicis (and not by the branches of this deep branch that innervate the dorsal and ventral interossei: Fig. 4; Bello-Hellegouarch et al., submitted). Moreover, contrary to the statements of some authors (e.g., Susman, 1994), our analyses revealed that the so-called ‘deep head of the flexor pollicis brevis’ of modern human anatomy is present in the vast majority of primates and that it corresponds to the flexor brevis profundus 2 of other mammals (Table 1; Diogo and Wood, 2011, 2012). For example, the structure designated as the flexor brevis profundus 2 in rats is the structure that is designated as ‘deep head of the flexor pollicis brevis’ of modern humans. Such a structure is also found in the vast majority of non-human primates, except for the New World monkeys in which this structure is either missing or, more likely, has fused with the flexor brevis profundus 1 component of the ‘superficial head of the flexor pollicis brevis’ of these monkeys. As Diogo and Wood (2011) argue, most authors have found a flexor brevis profundus 2 in the non-human and non-platyrrhine primates, but many have erroneously designated this structure either a component of the adductor pollicis or they have referred to it as the ‘interosseous volaris primus of H. enle’. Linscheid et al. (1991) have designated the adductor pollicis accessorius sensu the present paper as the ‘accessory adductor muscle’ or the ‘adductor pollicis accessory’, but their study is somewhat confusing because despite using this name they clearly consider that this muscle corresponds to the flexor brevis profundus 2 and not to part of the adductor pollicis, of other mammals (see, e.g., their Fig. 8). According to the authors, the adductor pollicis accessorius sensu the present paper is present in all eight modern human hands dissected by them, inserting onto the ulnar wing tendon of the thumb; the origin is from metacarpal 1 in four hands, from metacarpals 1 and 2 in two hands, from metacarpal 2 in one hand, and from the trapezium in one hand. Contrary to the hypothesis defended in the present paper, they thus consider that the ‘deep head of the flexor pollicis brevis’ of modern human anatomy corresponds to part of the oblique head of the adductor pollicis, and not to the flexor brevis profundus 2 of other mammals.

Moreover, they use the name ‘adductor pollicis, accessory oblique head’ to designate an extra head of the adductor pollicis that is present in six of the eight modern human hands dissected by them and that originates from metacarpal 2.

In summary, our comparative and phylogenetic analyses indicate that the flexor brevis profundus 2 has been present and has basically kept the same anatomical configuration from the LCA of eutherian mammals to H. sapiens, where it forms the so-called ‘deep head of the flexor pollicis brevis’. The names ‘deep head of the flexor pollicis brevis’ and ‘superficial head of the flexor pollicis brevis’ are thus inappropriate and in our opinion should be abandoned, because the former corresponds directly to the flexor brevis profundus 2 of other mammals while the latter derives from the flexor brevis profundus 1 (the opponents pollicis being also derived from the flexor brevis profundus 1: see above and Table 1). We propose that the ‘deep head of the flexor pollicis brevis’ and ‘superficial head of the flexor pollicis brevis’ are therefore designated as flexor brevis profundus 2 and as flexor pollicis brevis, respectively (see, e.g., Fig. 4; Table 1). As we have argued above, the ‘volar interosseous of H. enle’ of modern humans does not correspond to the flexor brevis profundus 2 of other mammals (i.e., it is not a true palmar interosseous), but instead it is very likely derived from the adductor pollicis (Fig. 9; Table 1: adductor pollicis accessorius; see below).

**Extensor pollicis brevis**

In modern humans, the extensor pollicis brevis, which is innervated by the posterior interosseous nerve, usually runs from the dorsal surface of the radius and the adjacent interosseous membrane to the base of the proximal phalanx of digit 1. Within the 200 adult modern human upper limbs examined by Kanef (1959, 1968, 1969, 1979, 1980a, b), the extensor pollicis brevis is missing in just over 1% of cases and in just over 5% of cases this muscle is reduced to a tendon connected to the tendon of the abductor pollicis longus or to ligaments adjacent to the insertion of this tendon. In most of the cases he examined, Kanef reported that the fleshy belly of the extensor pollicis brevis blends with the belly of the abductor pollicis longus. According to the ontogenetic studies of Lewis (1910), the abductor pollicis longus and extensor pollicis brevis usually only become separate entities late in modern human development. In our comparative sample, the only other group apart from modern humans with a distinct extensor pollicis brevis is the hylobatids. A separate extensor pollicis brevis was found in the hylobatids dissected by Bischoff (1870), Kohlbrügge (1890-1892), Duckworth (1904) and Michilsens et al. (2009) and by us (e.g., Fig. 7). The exception is Deniker (1885), who did not find a distinct extensor pollicis brevis in the gibbon foetuses dissected by
him. Contrary to the condition in modern humans, in hylobatids the extensor pollicis brevis usually does not extend to the proximal phalanx of the thumb, inserting instead onto the base of metacarpal I and/or the adjacent sesamoid or carpal bones. In gorillas (e.g., Hepburn, 1892; Straus, 1941a, b; Raven, 1950; Preuschoft, 1965; Sarmiento, 1994), a tendon of the abductor pollicis longus often inserts onto the proximal phalanx of the thumb and the term ‘extensor pollicis brevis’ has been used to describe this (N.B., in other great apes, including those dissected by us, the abductor pollicis longus usually inserts onto metacarpal I and/or onto carpal bones: see Diogo and Wood, 2011). However, as Huxley (1864), Macalister (1873), Bischoff (1880), Deniker (1885), Tuttle (1970), Kaneff (1979, 1980a, b), and Aziz and Dunlap (1986) have stressed, in gorillas the tendon going to the proximal phalanx of the thumb is the result of a bifurcation of the tendon of the abductor pollicis, the other branch of this tendon usually going to the metacarpal I (Fig. 8). Our dissections corroborate this. Thus, contrary to the condition in modern humans and hylobatids, in gorillas and in other primates there is no separate extensor pollicis brevis muscle (i.e., a distinct belly separated from abductor pollicis longus). It should moreover be noted that in the literature reviews carried out by Straus (1941a, b) and Sarmiento (1994), for gorillas they found that in just over half of the cases the abductor pollicis longus only extends as far as the proximal phalanx of the thumb.

In summary, modern humans are peculiar because they have a distinct extensor pollicis brevis that attaches to the proximal phalanx of the thumb, hylobatids are peculiar because they have a distinct extensor pollicis brevis that usually attaches to the base of metacarpal I and/or to adjacent bones, and gorillas are peculiar because in about half of the cases one of the two tendons of the abductor pollicis longus attaches to the proximal phalanx of the thumb. According to our dissections and review of the literature, in chimpanzees, orangutans and in non-hominoid primates the abductor pollicis longus usually has two tendons, but with the exception of one of the 20 chimpanzees reviewed by Keith (1899), these do not extend to the proximal phalanx of the thumb.

Conclusions

Our comparative and phylogenetic analyses indicate that the forearm muscles in primates usually number between 18 and 19 (Table 1). Two of the 19 muscles predicted to be plesiomorphically present in primates may be missing in some groups (e.g., the epitrochleoeancon is usually absent in hominoids except Pan and the anconeus is usually absent in Hylobates). Modern humans, because they usually lack the epitrochleoeancon but have two muscles going to the phalanges of the thumb (flexor pollicis longus to the distal and extensor pollicis brevis to the proximal), have more forearm muscles (i.e., 20) than any other primate studied by us (Table 1). Hylobatids also have a flexor pollicis longus and an extensor pollicis brevis, but as stated above they normally lack an anconeus, so they have 19 forearm muscles (Table 1). With respect to the hand muscles, phylogenetically plesiomorphic primates such as strepsirrhines and Tarsius usually have more than 30 muscles, but modern humans usually have only 21 muscles (Table 1). The hand muscles that modern humans have lost relative to phylogenetically plesiomorphic primates (i.e., contrahentes, intermetacarpales and interossei accessorii) attach to digits 2–5 (Table 1). The hand muscles that are conserved as separate structures in modern humans are those that insert onto the thumb. Modern humans usually also have an additional pollical structure that may also be present in gorillas and chimpanzees, which is often designated as ‘musculus interosseus volaris primus of Henle’ but should be designated as musculus adductor pollicis accessorius (Table 1).

Contrary to what is sometimes suggested in the literature, none of the muscles and muscle bundles in the modern human forearm and hand are unique to modern humans. Nonetheless, it is probably not a coincidence that the three derived structures found in modern humans and in only one or two other primate genera (i.e., adductor pollicis accessorius is also found in some Pan and Gorilla: flexor pollicis longus and extensor pollicis brevis also found in Hylobates) all involve the thumb. In fact, this is consistent with the hypothesis that movements of the thumb played an important role in human evolution. Marzke et al. (1998) suggested that the flexor pollicis longus and extensor pollicis brevis may have co-evolved to enable the members of the subtribe Hominina to maintain the metacarpophalangeal joint in extension while flexing the distal phalanx of the thumb as occurs in stone tool making and particularly usage. However, the presence of the flexor tendon attachment site on distal phalanges of all known fossil taxa of the subtribe Hominina suggests that some of this musculature was present early in human evolution and indeed it may be the primitive condition for the Pan-Homo LCA.

The functional significance of the adductor pollicis accessorius is more obscure, because this structure usually connects the ulnar side of the base of metacarpal I to the wing tendon of the extensor apparatus of digit 1. It is not very substantial and it is difficult to see (e.g., Morrison and Hill, 2011) how it could confer substantial biomechanical advantage across the joints of the thumb. Detailed comparative morphological and functional analyses, ideally including electromyographic studies, should be carried out in modern humans and also in gorillas and chimpanzees in order to

Figure 9. Simplified scheme showing our hypothesis about the evolution of the adductor pollicis accessorius (or ‘interosseous volaris primus of Henle’ of modern human anatomy): A) First stage of evolution, with a mainly undivided oblique head of the adductor pollicis (OH); B) Second, hypothetical stage of evolution, with the oblique head plus an additional bundle (AB) that has an origin separated from the main body of this head but still a common insertion together with that main body; C) Third, hypothetical stage of evolution, in which the insertion of the additional bundle is also somewhat separated from the main body of the adductor pollicis, forming an almost completely differentiated PPI; D) Fourth, hypothetical stage of evolution, showing a PPI that is even more lateral (radial) and thus even more separated from the main body of the oblique head of the adductor pollicis, resembling a PPI configuration that is commonly found in modern humans (DP, distal phalanx of digit 1; MI, metacarpal 1; PP, proximal phalanx of digit 1).
better understand the functional and evolutionary significance of this enigmatic structure. In addition, further studies of more specimens of other primate taxa are needed to check if this structure may be present in at least some specimens of non-hominin taxa as well.

The adoption and consistent use of the names proposed in this paper is not a mere nomenclatural detail: it is a return to an old, and Darwinian, tradition in which it is important to understand the phylegony and homology of each and every anatomical structure. It is also a way to stress that modern humans usually have 11 muscles (abductor pollicis longus, extensor pollicis brevis, extensor pollicis longus, flexor pollicis longus, abductor pollicis brevis, flexor pollicis brevis, opponens pollicis, adductor pollicis, dorsal interosseus I, adductor pollicis accessorius, and flexor brevis profundus) attached to metacarpal I and the pollical phalanges, and not nine as it often stated in atlases and textbooks. We hope that this paper will attract the attention of the authors of human anatomy atlases and textbooks and will thus result in the inclusion, in these atlases and textbooks, of information about the muscles adductor pollicis accessorius and the muscles flexor brevis profundus 2.

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Forster, A., 1917. Die mm. contrahentes und interossei manus in der Säugetierreihe (abductor pollicis longus, extensor pollicis brevis, extensor pollicis longus, flexor pollicis longus, abductor pollicis brevis, flexor pollicis brevis, opponens pollicis, adductor pollicis, dorsal interosseus I, adductor pollicis accessorius, and flexor brevis profundus) attached to metacarpal I and the pollical phalanges, and not nine as it often stated in atlases and textbooks. We hope that this paper will attract the attention of the authors of human anatomy atlases and textbooks and will thus result in the inclusion, in these atlases and textbooks, of information about the muscles adductor pollicis accessorius and the muscles flexor brevis profundus 2.


