

Regional Phylogenetic Analysis of the Myology of Primates and Correlates in the
Human Skeleton

by Michael William Kern

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Bernard A. Wood

University Professor of Human Origins and Professor of Human Evolutionary Anatomy

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Dedication

The author wishes to dedicate this work to his parents, David and Mary Jo Kern.

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Abstract of Thesis

Regional Phylogenetic Analysis of the Myology of Primates and Correlates in the Human Skeleton

Morphological studies of hard tissue are the only available method with which to examine phylogenetic relationships among fossil taxa. Recently, Diogo and Wood (2011) demonstrated the value of myological data for use in phylogenetics and that they provide an accurate phylogenetic signal, perhaps more accurate than signals provided by hard tissue analyses. My goal in the present work was to elucidate how useful examination of these soft tissue characters can be to the study of human origins. This was a two-fold project.

The fossil record of our subtribe, Hominina, is often fragmentary. As such, it would be valuable to know which body regions provide the most accurate and reliable phylogenetic signals. In Chapter 2 I attempt to determine this by sorting the characters defined by Diogo and Wood (2011) by body region and performing seven cladistic analyses. The cranial region provides the most accurate reconstructions, as well as the most efficient analysis in terms of characters required for accurate reconstruction.

Being able to directly reconstruct these muscle characters in fossils would be invaluable to the study of human origins. In Chapter 3, I attempt to macroscopically recover the ninety-two characters that exhibit a direct relationship to hard tissue. I effectively recover 23 of these characters, which was expected given previous attempts by other authors. These 23 characters provide a phylogenetic reconstruction better than most of the body regions, and are therefore a promising start to future studies.

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Chapter 1: Introduction

Phylogenetics in Primate and Fossil Studies

Many attempts have been made to discern the relationships that exist between the different clades within the extant members of the primate order. In the past, these analyses have been strictly morphological. However, since the rise of molecular studies, and in particular the idea of the “molecular clock”, morphological studies of phylogenetic relationships have largely begun to be replaced (Zuckerkandl and Pauling, 1962). This is due to the immense amount of data one can include in a DNA driven analyses compared to the amount of morphological characters that can be coded for phylogenetic studies. Recent studies have indicated that hard tissue morphological and molecular analyses support each other, and that more similarities than differences are found between those methods (Shoshani, 1986; Shoshani et al., 1996). A recent study by Diogo and Wood (2011) provided a robust analysis of soft-tissue myological characters for primate phylogenetics, and those results largely agree with the molecular studies as well. However, these different lines of inquiry do not provide results that are in complete agreement in some aspects, and so conclusions must be drawn from all lines of evidence available.

Shoshani et al. (1996) especially point out the disagreement between fossil and molecular analyses of phylogenetic relationships with regards to the placement of tarsiers. The authors, as well as Diogo (2011), argue that this is not an indication of the methods providing different phylogenetic signals, but that the morphological data is being incorrectly assessed (Shoshani et al., 1996; Diogo, 2011). Likewise, the assumptions behind many of the molecular studies have been called into question, which indicates a

continued need for morphological examination of relationships (Schwartz and Maresca, 2006; Diogo, 2011). This means researchers must change the ways in which the morphological data found in the fossil record are analyzed. Hence, Diogo undertook the study of primate phylogenetics using myological characters, the data of which are employed in the present study (Diogo, 2011).

Most cladistic analyses of primates and, more specifically, great apes, agree that chimpanzees are humans' closest living relatives (Shoshani, 1986; Shoshani et al., 1996; Steiper and Young, 2006; Fabre et al., 2009; Arnold et al., 2010). Though there are discrepancies in the timing of this split depending on the evidenced used, it is likely that this occurred 5-7 million years ago (Kumar et al., 2005; Stone et al., 2010). Thus, the characters that distinguish these two taxa are the same that may differentiate between the fossil species of that period. Well-known examples of the use of traits seen in extant humans and chimpanzees to assess the relationships and functions of extinct fossil species are seen in discussions of hominin dentition by Lockwood and Fleagle (1999), Lovejoy et al. (2009), and Suwa et al. (2009) among others, as well as the examination of locomotor patterns as seen in Zollikofer et al. (2005), Lovejoy et al. (2009), and Richmond and Jungers (2009) among others. The traits of fossil Hominina (Fig. 1) members discussed with regard to their presence or absence in extant humans and chimpanzees are not limited to these two examples. These merely serve to illustrate how important the differences between these two taxa are to the study of fossil members of the subtribe Hominina. Though the preceding examples are generally functional differences between the taxa, these differences are also the type of information which can be useful to phylogenetic analyses of the fossil Hominina evidence.

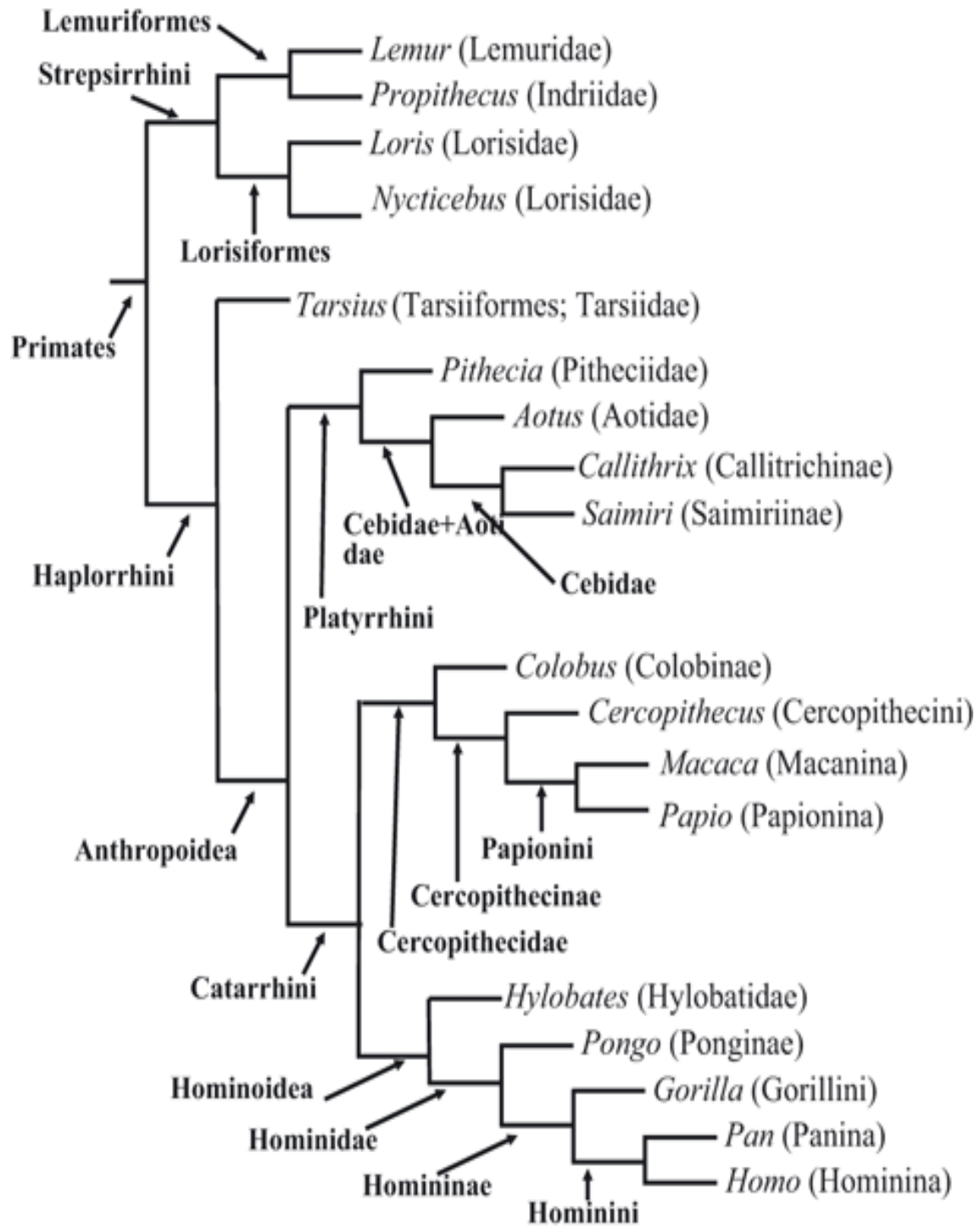


Figure 1: From Diogo and Wood (2011). The accepted molecular phylogenetic analysis of primates, with more specific clades labeled. Originally from Arnold et al. (2010), showing only the 18 clades of interest to this study.

Soft Tissue in Phylogenetics

As stated, soft-tissue characters can be of great use to phylogenetic analyses. Because of the disagreement between the results of different methods of phylogenetic analysis, multiple analyses of the same clades can strengthen conclusions about those relationships. As is the case between hard tissue and molecular data, soft tissue and hard tissue analyses may also provide different phylogenetic results (Gibbs et al., 2000, 2002; Diogo, 2004). In their most rudimentary addition to the field, myological characters thus provide one more method through which these relationships can be tested.

In fact, myological characters may provide a better indication of phylogenetic relationships than hard tissue characters currently do. Muscle tissue often has “morphogenetic primacy” over skeletal material, which explains why the signals generated by these characters may provide results more like molecular phylogenetic reconstructions (Witmer, 1995). These characters are both useful for inferring high-level relationships in several groups, as well as less variable than hard-tissue characters often are (McKittrik, 1991; Gibbs et al., 2000, 2002; Diogo, 2004). The largest of scope and most recent work on this in primates was done by Diogo and Wood (2011), whose data is largely utilized for the present analyses. Theoretically, this allows analyses to be performed from fewer individual specimens while still using data that is useful for inferring phylogeny. This resource should be explored more in cladistics.

Predicting how muscles change the form of the underlying skeletal material would allow us to infer these myological characters from said skeletal material. This would require further understanding of the relationship between these two tissue types. The ability to infer myological characters from skeletal material would allow use of these

characters in fossil studies, in turn allowing us to further strengthen conclusions about the relationships of fossil species. Such studies would be invaluable to the field of hominid paleobiology and human evolution.

Soft Tissue Reconstructions in Skeletal and Fossil Studies

Several systematic attempts have been made to reconstruct soft tissues, specifically muscles, from skeletal material. These reconstructions have occurred in studies of very different clades as well as with very different levels of resolution and reasoning. The less intense reconstruction attempts are those such as assuming increased muscle mass as associated with a suite of other characters, as seen in analyses of *Paranthropus* masticatory function (McCollum, 1998; Strait et al., 2005). Such analyses do not examine the direct relationship between muscle tissue and the skeletal elements being studied, and so though such reconstructions are not necessarily illogical by any means, their reconstruction of muscle characters is through indirect means. It also must be noted that attempts at reconstructing muscle tissue in fossil primates studies are limited by the availability of specimens and the destructive techniques often required for more direct reconstructions.

More specific studies about the relationships between bone and myological tissue have been performed in extant lower mammals. Macroscopically, it has been shown that the presence of a muscle can greatly influence whether certain landmarks develop in associated bones (Nowlan et al., 2010). It is not just the presence of the muscle that determines this morphology, however, as placement of the muscle has been shown to affect bone development through surgically moving the masseter muscle in developing rabbits (Bayram et al., 2009). This illustrates the aforementioned morphogenetic primacy of

muscle tissue compared to bone (Witmer, 1995). It provides some ability to infer muscle from skeletal material, but may be confounded by the complicated relationships of multiple muscles with individual skeletal landmarks in some regions of the body.

Previous macroscopic evaluations of muscle attachment sites and osteological landmarks show disagreement as to how well these characters are recovered. Studies of the kiwi bird illustrate little macroscopic correlation between these attachment sites and the underlying osteology, recovering only 23% of the known hindlimb characters and only 29% of the known wing musculature characters from an analysis of hard tissue (McGowan, 1979; 1982). This is in contrast to a 83% and 77% tenuous correlation rate between muscle attachment and any osteological feature found in *Canis* and *Ursus* respectively (Bryant and Seymour, 1990); this same study mentions 34% and 26% correlation rates where the “full extent of the attachment site can be inferred from the osteological feature” which is more akin to the reasoning used in the current analysis. Both studies recovered myological characters from skeletal material at a macroscopic level, and they provide an exceptional starting point for other more rigorous types of examination. Definitive recovery of characters at these rates from fossil human ancestors would provide invaluable information to the study of human origins that is unavailable presently.

Moreover, microscopic and histological studies help to recover more myological characters from hard tissue analyses. For instance, scanning electron microscopy (SEM) and histological sectioning of tendon attachment sites have shown that there is at least some indication that the force and/or mass of the associated muscle can be inferred from markings on the bone (Benjamin et al., 2002). Histological sectioning has also shown that muscle attachment sites can be seen in bone when there is no macroscopic evidence of that

attachment (Hieronymus, 2006). Together these show that at least certain types of muscles can reliably be discerned from skeletal material, though the reconstruction will be incomplete with the methods presently accessible. The relationship between muscle tissues and their bone correlates must be further examined, as a complete picture would allow direct reconstruction of soft tissues in extinct species, where we would otherwise have very little direct evidence of any structure beyond the skeletal system of these animals. For instance, if within the 166 myological characters used by Diogo and Wood (2011) one would be able to recover one third of them macroscopically (as suggested by previous studies: see above) from fossil members of our subtribe Hominina, functional and phylogenetic studies would both benefit immensely from such data.

Layout of this Work

This work is therefore a two part analysis of primate phylogenetics. First, the dataset from Diogo and Wood (2011) is re-worked to provide a cladistic analysis for each of seven body regions. This provides an analysis of what, if any, body regions provide more accurate phylogenetic reconstructions, i.e. a stronger phylogenetic signal. The second portion of the work is a case study in myological tissue reconstruction in complete modern human skeletons, which will provide an indication of how many of the myological characters from Diogo and Wood (2011) might be macroscopically recoverable in key fossils of our subtribe Hominina. All characters defined by Diogo (2011) that attach directly to bone in a human body are examined to discern whether they can be recovered from skeletal material macroscopically, and whether further analysis through different

methods, including histology and microscopy, would be useful to the study of the primate fossil record.

Chapter 2: Regional Phylogenetic Analysis of the Myology of Primates

Background

The study of primate cladistics benefits from examining the largest amount of evidence in as many ways as possible (see above). Often, the larger the scope of an analysis is, the more absolute instances of homoplasy will be present in that analysis – the proportion of homoplastic characters to homologous characters may remain low, however. By regionalizing the analysis and limiting the number of characters present, it is theoretically possible to minimize the proportion of homoplastic character state changes, and perhaps produce a more parsimonious cladistic analysis. Regionalization also makes these analyses more applicable to fossil Hominina studies, as the fossil record of most species are largely fragmentary, and so only certain body regions are available for phylogenetic reconstructions (Richmond and Jungers, 2008). These analyses should indicate whether a fossil species can be confidently included in a phylogenetic analysis based on the available body regions.

The original Diogo and Wood (2011) dataset grouped muscles by ontogenetic region. Because of the application of this data to fossil studies in the section that follows, and the importance of the muscle-bone interaction for such studies, these characters are reorganized into superficially functional muscle groups. Direct evidence of muscle characters usable in phylogenetic reconstructions are largely at attachment sites of those muscles, which are correlated with the functional aspect of the muscle instead of the ontogenetic (see following section for an explanation of these relationships). Therefore, an ontogenetically “pectoral” muscle that inserts onto or originates from the humerus will

likely affect the form of the humerus, and so to be of use in fossil studies must be treated as an “arm” muscle. Likewise, a “forearm” muscle that originates from the humerus will also be treated as an “arm” muscle. Therefore, muscle characters can be used in two or more regions for the following analyses (see below for examples of characters that have been moved into multiple regional datasets) if the characters involve attachments to bones of two or more different regions. However, if a muscle has an origin from or insertion onto a bone but that attachment is not affected by the character in question, then the unaffected attachment did not necessitate inclusion of that character in that associated bone region. For changes in superficial muscles or in characters that do not pertain to a bony attachment, the body region where that change is manifested is used to group the muscle (hence the use of “attachment” instead of the more specific “origin” and “insertion” below). Use in multiple datasets is mostly seen in characters that are contingent on the presence or absence of a muscle, as changes in those characters will affect both the insertion and origin of that muscle.

These reconstructions should indicate whether there are specific, functionally regional, evolutionary trends in muscle anatomy within the primate order. Based on the homoplasy seen in these regions when using the full dataset, the pectoral region is predicted to be the least homoplastic of the seven regions used in this analysis and therefore to provide the shortest and most effective cladistic analysis. Nine unambiguous non-homoplastic character state changes occur in this region compared to only six homoplastic changes, making it the only region in which the number of non-homoplastic changes was greater than the number of homoplastic changes in the same region (Diogo and Wood, 2011).

Methods

The myological characters used in this analysis were taken from Diogo and Wood (2011); see Appendix I for a summary of the 166 characters used by those authors (Diogo and Wood, 2012). As explained above, in order to make the characters valuable to reconstruction in hard tissue materials and useful in fossil studies, several of the characters have been reassigned to different regions of the body. Such a change also provides a better examination of these characters with respect to the functional differences that they serve. For example, many of the forearm muscles from Diogo and Wood (2011) were only assigned to that region because of the ontogeny of those muscles, and have been reassigned to the hand in the current analysis. These muscles are of great importance in the function of human (especially the thenar region and other thumb muscles) and gibbon hands, which the present analysis effectively recovers. Reassignment was done based on where any possible difference would be realized on a bone.

This reassigning of characters required new regions to be used, and made some of the original regions inconsequential. Regions used in this analysis are cranial (all bones of the cranium except the mandible), mandibular, hyoid, pectoral (the scapula, clavicle, sternum, and ribs), arm (only the humerus), forearm (both radius and ulna), and hand (all hand and wrist bones). “Ventral (volar) forearm” and “dorsal forearm” from Diogo and Wood (2011) have been collapsed into the forearm region in this analysis. The original analysis did not have a cranial region, which is included here to account for those muscles that attach directly to any of the cranial bones that are not the mandible. Likewise, the “branchial” and “hypobranchial” muscle groups have been dropped for this analysis, with

those muscles entirely reassigned by attachment sites when appropriate. A list of all changes from the original dataset is below.

Cladistic analyses were performed on these seven datasets, using the same coding used by Diogo and Wood (2011). All analyses were parsimony based. The search for the most parsimonious trees used Nona and Winclada (version 10.00.08; Nixon, 2002) with the “multiple TBR + TBR (mult*max*)” option and an “unconstrained search”, with 10000 maximum trees to hold, 1000 replications, and 1000 starting trees per hold and 0 random seed. Bootstrapping and Bayesian analyses were not performed on the datasets at hand.

In all analyses, all characters have only two states (excepting ambiguous states or the inapplicability of a character to a given taxon) except the multistate ordered characters 60, 68, 124, 136, 138 and 149, and the unordered multistate characters 129 and 162. See Diogo and Wood (2011) for reasoning as to the designation of ordered and unordered for these characters. A terminal taxon, “Outgroup”, as well as a character “number 0” (character state 0 for all taxa) was included in these analyses. Both of these are due to the way Winclada constructs character matrices and roots the trees in heuristic analyses by always forcing the first taxon that is listed in the matrix to appear in the root of the tree. Including “Outgroup” created a situation in which one of the other non-primate taxa (*Rattus*, *Cynocephalus*, and *Tupaia*) were not taken as the most plesiomorphic taxon for any or all trees. For all parsimony analyses, *Rattus*, *Cynocephalus*, and *Tupaia* were assigned as unconstrained outgroups and all other taxa were included in the ingroup.

The first dataset consists of all the characters defined by Diogo (2011) that are associated with the cranial bones. This includes characters 6-8, 10, 13, 15-21, 23-38, 41, 44, 48, 49, 60 and 61. The second dataset consists of all characters that are associated with

the mandible, and includes characters 1-3, 5, 9, 14, 16, 17, 20, 22-25, 39, 40, 53 and 60. The third dataset consists of all characters that are associated with the hyoid bone (sometimes indirectly through fascial, tendonous, or cartilaginous contact), and includes characters 10-12, 15, 41, 42, 50-65 and 67. The fourth dataset consists of all characters associated with the bones of the pectoral region, and includes characters 25, 43-47, 49, 63-80, 83-88, 94, 95, 97, 98, 102 and 107. The fifth dataset consists of all characters associated with the humerus, and includes characters 80, 81, 83, 87, 89-93, 96, 99, 100, 102, 107, 110, 119, 120, 123, 124, 154-158 and 161. The sixth dataset consists of all characters associated with the radius and/or ulna, and includes characters 92, 101, 103-106, 108-110, 113, 114, 117-120, 123, 124, 152, 154-157, 161, 163 and 166. The seventh dataset consists of all characters associated with bones of the hand and wrist, and includes characters 112, 115-118, 121, 122, 125-153, 158-160, 162, 164 and 165.

Figures presented of trees generated from the above datasets are “majority fools” consensus of all the most parsimonious trees for each dataset.

Reassigned Characters

From the “mandible” region: #6 The *tensor tympani m.* attaches to the sphenoid bone and the auditory canal instead of the mandible, so it is now classified as “cranial”. #7 The relationship between the chorda tympani and the *tensor tympani m.* again involves attachments on cranial bones, not the mandible, and so it is also a “cranial” character. #8 The posterior portion of the *temporalis m.* attaches to the cranial bones, not the mandible, and is thus designated a “cranial” character.

From the “hyoid” region: #10 The *stylohyoideus m.* attaches to both the hyoid bone, and the styloid process of the cranium, and is used in both the “hyoid” and “cranial” regions. #13 The *stylohyoideus m.* only has a bony attachment on the styloid process, so it is designated as a “cranial” character. #14 The attachment of interest of the *digastricus posterior m.* is on the mandible, and so this character is designated as “mandibular”. #15 The *jugulohyoideus m.* attaches to (or affects) both the hyoid bone and the mastoid process, and so this character is used in both “hyoid” and “cranial” regions. #16 The *platysma cervicale m.* connects the cranial bones and the mandible at a superficial level, and so is used in both of those regions. #17 The *platysma myoides m.* covers a large area, but the change in this character is a facial change, and so this character is used in both “mandibular” and “cranial” regions. #18 The change of interest in the *occipitalis m.* for this character occurs only on the cranial attachments, and so this character is designated as “cranial”. #19 The *auricularis posterior m.* has only cranial attachments, and so this is designated as part of the “cranial” region dataset. #20 The *mandibulo-auricularis m.* attaches to the mandible and the temporal bone, and so it is included in both the “mandibular” and “cranial” regions. #21 The *zygomatico-auricularis* attaches to both the zygomatic and temporal bones, and so it is designated as a “cranial” character. #22 The *risorius m.* attaches near the mouth and over the masseter muscle, and would mostly affect the mandible, so it is designated as “mandibular” for analysis. #23 and #24 Both the *sphincter colli superficialis m.* and the *sphincter colli profundus m.* are muscles of facial expression that spread over both the mandible and other cranial bones, and so these are classified as both “mandibular” and “cranial”. #25 The *sternofacialis m.* may affect the sternum, mandible, and facial regions, and so is designated as parts of the “pectoral”,

“mandibular”, and “cranial” regions. #26 The *interscutularis m.*, when present, only has connections on the cranium and so is a “cranial” character. #27, 28, 29, and 31 The *zygomaticus major m.* lies superior to the mandible, and so it is categorized as “cranial”. #30 Like the *zygomaticus major m.*, the *zygomaticus minor m.* attaches only superiorly to the mandible, and so is a “cranial” character. #32 The *frontalis m.* only attaches to the frontal bone, and so is a “cranial” character. #33 The *auricularis superior m.* attaches only on the temporal bone, and so it is a “cranial” character. #34 The *zygomatico-orbicularis m.* is a facial muscle superior to the mandible, and so this is a “cranial” character. #35 The *depressor supercillii m.* is a facial muscle superior to the mandible, and so is designated as “cranial”. #36 The *corrugator supercillii m.* is a muscle of the eye, and so is categorized as “cranial”. #37 The *levator labii m.* is a facial muscle that lies entirely superior to the mandible, and so is categorized as “cranial”. #38 The *depressor septi nasi m.* is a facial muscle that lies entirely superior to the mandible, and so is categorized as “cranial”. #39 The *depressor anguli oris m.* is a facial muscle of the inferior oral opening, attached to the mandible, and so is categorized as “mandibular”. #40 The *mentalis m.* is a facial muscle of the inferior oral opening, attached to the mandible and so is designated as a “mandibular” muscle.

From the “branchial” region: #41 The *stylopharyngeus m.* attaches to the styloid process of the cranium and the hyoid apparatus, and so is classified as “hyoid” and “cranial”. #42 The *ceratohyoideus m.* is connected to the apparatus of the hyoid and so is classified as a “hyoid” muscle. #43 The *spinotrapezius m.* corresponds to a portion of the *trapezius m.* that is entirely associated with the scapula, and so is designated as a “pectoral” character. #44 The *cleido-occipitalis m.* attaches to both the clavicle and the occipital bone,

and so is included with both “cranial” and “pectoral” datasets. #45, 46, and 47 The *trapezius m.* attaches to the clavicle and scapula, and so these three characters are classified as “pectoral”. #48 The *trapezius m.* also attaches to the cranium, and so this is designated as a “cranial” character. #49 The *sternocleidomastoideus m.* attaches to the sternum, clavicle, and mastoid process, and so is designated as both “pectoral” and “cranial”. #50 The *constrictor pharyngis medius m.* is a muscle of the throat region, and contacts only the hyoid bone, and so is classified as a “hyoid” character. #51 The *cricothyroideus m.* attaches to the hyoid bone and the thyroid cartilage, and so is classified as a “hyoid” character. #52 The *thyroideus transversus m.* is a laryngeal muscle and so is most likely to affect the hyoid bone; therefore, it is classified as a “hyoid” character. #53 The *pterygopharyngeus m.* is part of the superior constrictor pharyngeal muscles and so may affect both the hyoid apparatus as well as the mandible, and so is included in both “hyoid” and “mandible” datasets. #54 The *thyroarytenoideus m.* is a laryngeal muscle, which is most likely to affect the hyoid bone, and so is classified as a “hyoid” character. #55 The *arytenoideus obliquus m.* is a laryngeal muscle, which is most likely to affect the hyoid bone, and so is classified as a “hyoid” character. #56 The *cricoarytenoideus posterior m.* is part of the laryngeal muscles, and so this character is classified as “hyoid”.

From the “hypobranchial” region: #57 The *geniohyoideus m.* contacts the hyoid bone, and so this character is classified as “hyoid”. #58 and 59 The *hyoglossus m.* (and therefore the *chondroglossus m.*) attaches to the hyoid bone and so these characters are designated as “hyoid”. #60 The *styloglossus m.* attaches to the cranium and hyoid, and the character state change affects its association with the mandible, so it is classified as a “hyoid”, “mandibular” and “cranial” character. #61 This character is also associated with

the *styloglossus m.*, but the state change does not affect the mandible, and so it is classified as only a “hyoid” and “cranial” character. #62 The *sternohyoideus m.* attaches to both the sternum and hyoid, but this change is only seen in the portion of the muscle that attaches to the hyoid bone, and so this character is designated as “hyoid”. #63 and #64 The *sternohyoideus m.* attaches to both the sternum and hyoid, and so this character is classified as both “hyoid” and “pectoral”. #65 and #67 The *omohyoideus m.* attaches to the hyoid and scapula bones, and so this character is classified as both “hyoid” and “pectoral”. #66 Though the *omohyoideus m.* has attachments on the hyoid and scapula, this character only affects the clavicle and so is designated as “pectoral”.

From the “pectoral” region: #80 The *pectoralis major m.* inserts onto the scapula and/or the humerus, and so this character is designated as both “pectoral” and “arm”. #81 The insertion of the *pectoralis major m.* associated with the *biceps brachii m.* is only on the humerus, and so this character is classified as “arm”. #82 The insertion of the *pectoralis major m.* is the only attachment affected by this change, and so this character is classified as “arm”. #83 The *pectoralis minor m.* inserts onto the humerus and/or the scapula, and so this character is classified as “pectoral” and “arm”. #87 The *teres minor m.* attaches to both the scapula and humerus, therefore this is designated as both a “pectoral” and “arm” character. #89 The *lattisimus dorsi m.* and the *teres minor m.* both attach to the scapula and the humerus, and so this character is designated as both “pectoral” and “arm”.

From the “arm” region: #92 The *dorsoepitrochlearis m.* inserts onto the ulna and/or the humerus, and so this character is classified as both a “forearm” and “arm” character. #94 The origin of the *dorsoepitrochlearis m.* is associated with the scapular region to different degrees, and so this character is designated as “pectoral”. #95, #97 and #98 The

long head of the *triceps brachii m.* attaches to the scapula, and so these characters are designated as “pectoral”. #101, #104, #105 and #106 The insertions of the *biceps brachii m.* are associated with the ulna and radius, and so these characters are classified as “forearm”. #102 The *biceps brachii m.* originates from the scapula and/or the humerus, and so this character is classified as both “pectoral” and “arm”. #103 The *biceps brachii m.* and the *flexor digitorum superficialis m.* are only associated in the forearm, and so this character is designated as “forearm”. #107 The *coracobrachialis m.* attaches to both the humerus and scapula, and so this character is classified as both “pectoral” and “arm”.

From “ventral (volar) forearm” region¹: #110 The *flexor digitorum profundus m.* originates from the medial epicondyle of the humerus and/or the forearm bones, so this character is classified as “arm” and “forearm”. #111 This character has been dropped from this analysis, as it deals with innervation of a muscle as opposed to the state of the myological tissue itself. #112 The *flexor digitorum profundus m.* inserts on the hand, so this character is classified as “hand”. #115 and #116 The *flexor digitorum superficialis m.* inserts onto the hand as well, and so these characters are both classified as “hand”. #117 and #118 The *palmaris longus m.* attaches to both the forearm bones and the hand, and so it is classified as both “forearm” and “hand” for these analyses. #119 The *flexor carpi ulnaris m.* originates from the humerus and/or the ulna, and so this character is classified as “arm” and “forearm”. #120 The *epitrochleoanconeus m.*, when present, attaches to both the ulna and the humerus, and so this character is classified as both “arm” and “forearm”. #121 and #122 The *flexor carpi radialis m.* inserts onto the fingers, and so these characters are classified as “hand”. #123 The *flexor carpi radialis m.* originates from the humerus and/or

¹ Changes from “ventral forearm” to “forearm” are not included here.

ulna, therefore this character is classified as both “arm” and “forearm”. #124 The *pronator teres m.* originates from the humerus and/or ulna, therefore this character is classified as both “arm” and “forearm”.

From the “hand” region: no characters from the “hand” region used in Diogo and Wood (2011) were changed for this analysis.

From the “dorsal forearm” region²: #152 The *brachioradialis m.* inserts onto the radius and/or trapezium, so this character is used for both “forearm” and “hand” datasets. #153 The *extensor carpi radialis m.* inserts onto exclusively hand/wrist bones, and so this character is classified as “hand”. #154 The *brachioradialis m.* attaches to both the humerus and radius, and so this character is designated as both “forearm” and “arm”. #155 The ulnar head of the *supinator m.* attaches to both the forearm bones as well as the humerus, and so this character is classified as both “forearm” and “arm”. #156 The *extensor carpi ulnaris m.* originates from the humerus and/or the ulna, and so this character is designated as both “forearm” and “arm”. #157 The *anconeus m.* attaches to both the humerus and the ulna, and so this character is classified as both “forearm” and “arm”. #158 The *extensor digiti quarti m.* attaches to both the humerus and hand, and so this character is classified as both “arm” and “hand”. #159 and #160 The *extensor digiti minimi m.* inserts on the digits, and so these are classified as “hand” characters. #161 The *extensor digiti minimi m.* originates from the humerus and/or the ulna, therefore this character is used in both “forearm” and “arm” datasets. #162 The *extensor indices m.* inserts on the digits, and so this character is classified as a “hand” character. #164 The *extensor pollicis longus m.* and *extensor indicis m.* insert on the digits, and so this is designated as a “hand” character. #165 The *abductor*

² Changes from “dorsal forearm” to “forearm” are not included here.

pollicis longus m. inserts on the thumb, and so this character is classified as a “hand” character. #166 The *extensor pollicis brevis m.* attaches to both the thumb and the forearm bones, and so this character is classified as both “hand” and “forearm”.

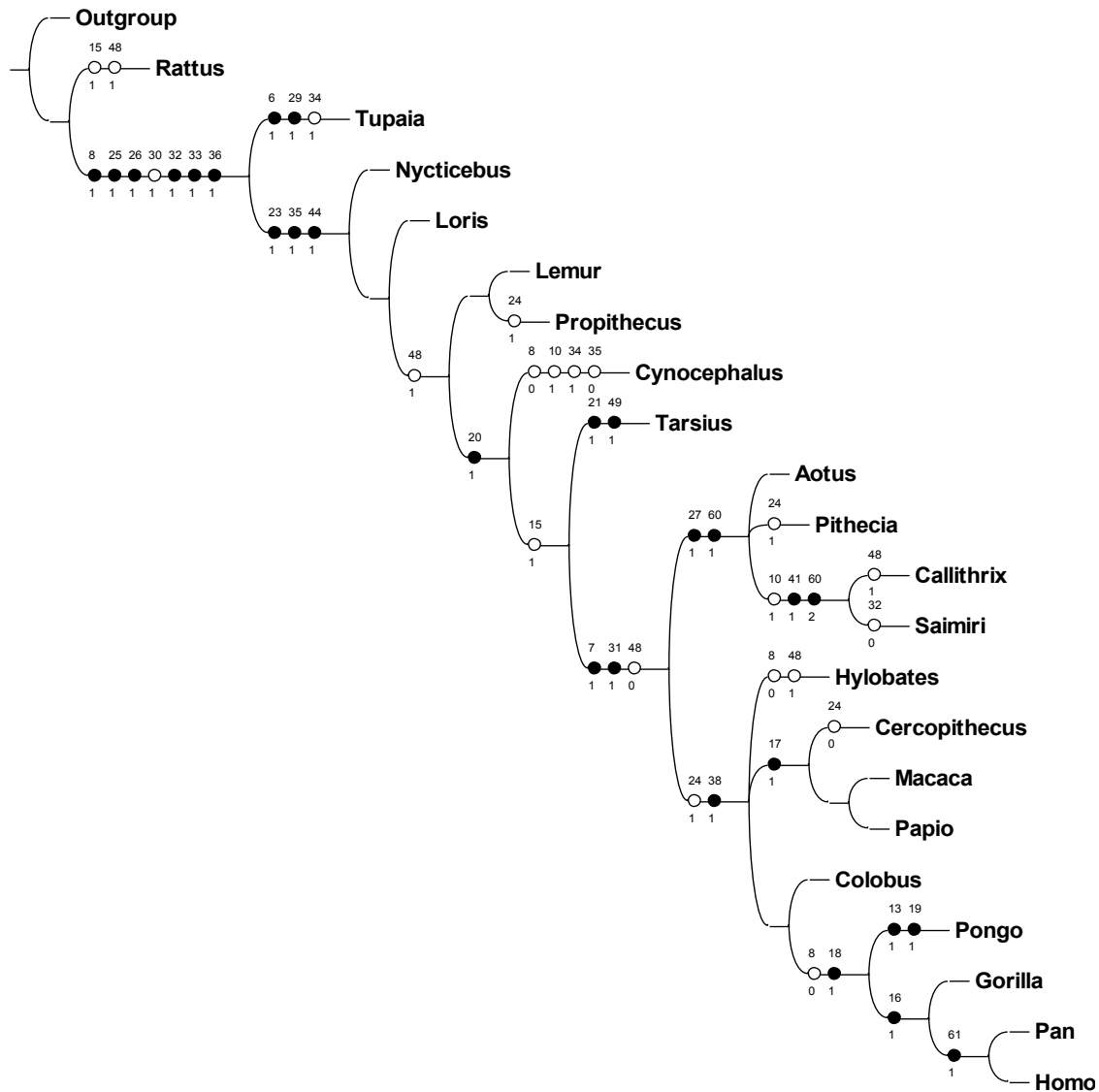


Figure 2: “Consensus majority” tree of 12 most parsimonious trees from the 34 characters of the “cranial” dataset (L:56, Ci:62, Ri:79). Unambiguous homoplastic (open dot) and non-homoplastic (black dot) character state changes are shown along branches. Correctly recovers 13 of the 19 clades (68.4%), Hominini, Homininae, Hominidae, Papionini, Cercopithecinae, Catarrhini, Cebidae, Platyrrhini, Anthropoidea, Haplorrhini, Lemuriformes, Cynocephalus+Primates (Primateomorpha) and Tupaia+Cynocephalus+Primates (Euarchonta). The only clades shown in this figure that are not represented in 100% of the most parsimonious trees are Colobus+Hominidae (present in 66% of the trees), the Catarrhini (75%), Platyrrhini (75%) and the Haplorrhini (58%).

Results

The regionalization of the myological characters defined by Diogo and Wood (2011) yielded less definitive and accurate phylogenetic results than an analysis of the full character set did. Here, each of the seven “majority” consensus trees are shown (“majority” referring to the fact that clades shown were recovered in at least 50% of the most parsimonious trees generated for each dataset). Support for clades in all figures is shown by the proportion of most parsimonious trees the clade is recovered in (shown in the caption for each figure) as well as the number of character state changes supporting each clade (indicated by the parsimony branch length leading to that clade and the number of unambiguous character state changes).

The consensus tree generated by the cranial characters (Figure 2) recovered the largest proportion of clades represented in the original, 166 character, cladistic analysis from Diogo and Wood (2011) and accepted molecular studies (Fig. 1). Here, 13 of the 19 clades are effectively recovered (68.4%) in the cranial analysis using 34 characters. The second most effective reconstruction is through the use of the hand dataset (Fig. 8), which recovered 10 of the 19 clades (52.6 %) using 42 characters. These are the only analyses of the seven datasets that recover more than half of the correct clades. These are followed by the pectoral region at a 47.4% recovery rate with 9 of 19 clades recovered (Fig. 5) using 37 characters, which is surprising given the lower occurrence of homoplastic changes in that region (see below); then the hyoid region with 8 of 19 recovered (42.1%) using 23 characters; then the arm region (Fig. 6) with 6 of 19 clades recovered (31.6%) using 25 characters; then the mandibular region (Fig. 3) with 5 of 19 recovered (26.3%) using 17

characters; and finally the forearm region (Fig. 7) which only recovers 2 of 19 clades (10.5%) using 25 characters. This indicates that the cranial region is the best of those examined for myological phylogenetic analyses of primate fossils.

The above numbers also indicate that the cranial region is the most efficient region for recovering phylogenetic relationships in muscle tissue. From the numbers above, it required 2.62 characters per clade recovered. The next most efficient regions were the hyoid and mandibular regions, both of which recovered relatively few clades, but did so using on average fewer characters. They required 2.88 and 3.4 characters per clade recovered, respectively. Pectoral, arm, and hand regions were all comparable in efficiency, requiring 4.11, 4.17, and 4.2 characters per clade respectively. The forearm region again performed the worst, requiring on average 12.5 characters to recover a clade.

The cranial character set is particularly effective at recovering clades at the level of haplorrhini and above. In fact, the only differences between this character set and the molecular results are that *Hylobates* and *Colobus* are slightly misplaced. This indicates that cranial features, especially muscular features, are useful in elucidating relationships between monkeys and apes, and may indicate that this region would be most useful in fossil studies of those taxa. Below this level the percentage of clades effectively recovered drops dramatically, and so these characters become much less useful.

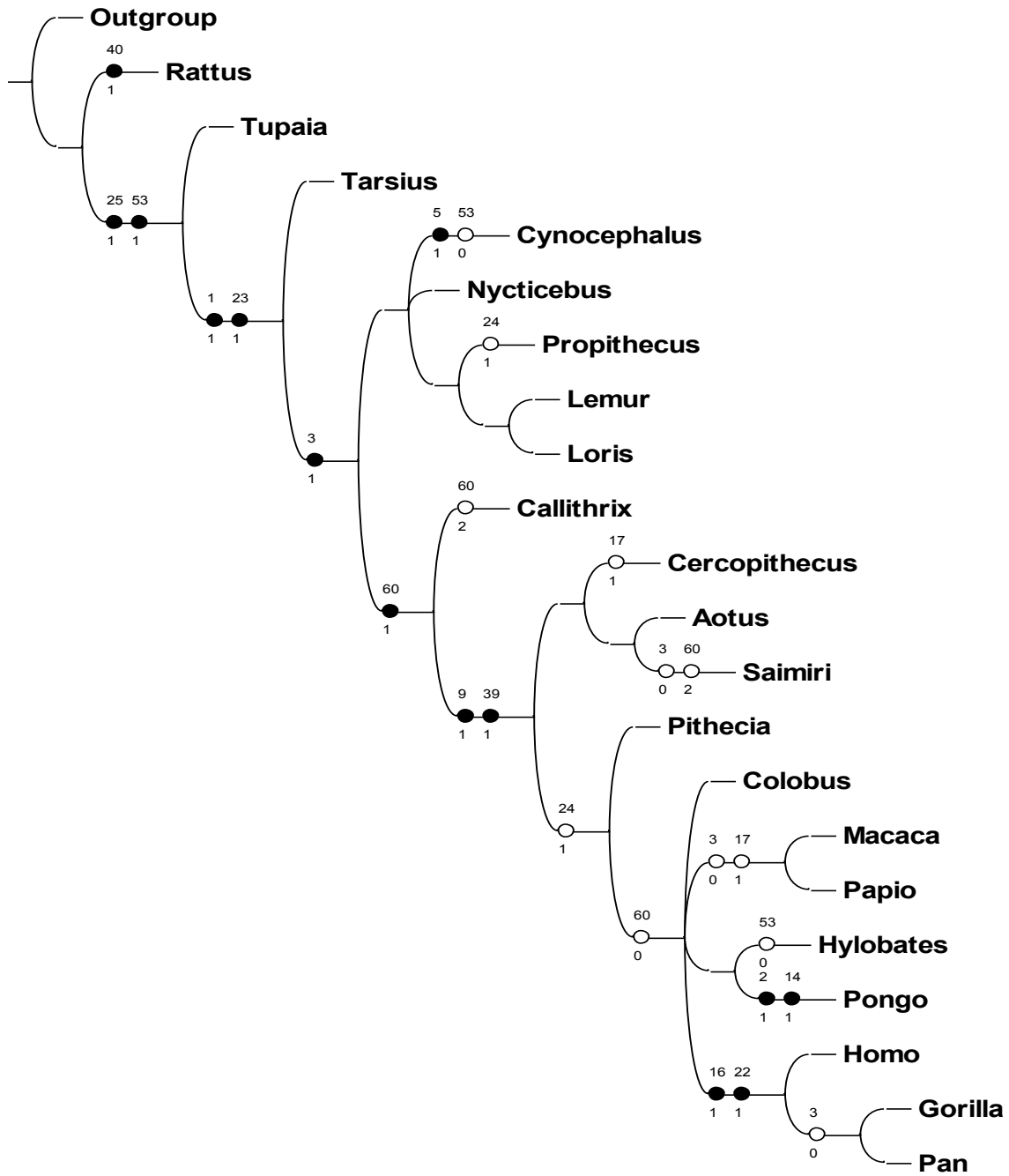


Figure 3: Mandibular consensus tree. From 20 most parsimonious trees (L:28, Ci:64, Ri:82). Unambiguous homoplasic (open dot) and non-homoplasic (black dot) character state changes are shown along branches. 5 of 19 clades correctly recovered (26.3%), Hominiinae, Papionini, Anthropeidea, Primatomorpha and Euarchonta. The only clades shown above not represented in 100% of the most parsimonious trees are the clade including everything except *Rattus*, *Tupaia* and *Tarsius* (recovered 75% of the time), the *Propithecus*, *Lemur*, and *Loris* (75%), the clade after the branching of, and excluding, *Cercopithecus* (80%), the clade occurring at the branching of, and including, *Pithecia* (80%), the clade including all Catarrhines except *Cercopithecus* (80%), and Hominiini (60%).

The other regions that are of value for primate or fossil studies are the hand and pectoral regions (Fig. 8 and 5, respectively). Though the hand region recovers more of the clades than the pectoral region, it recovers fewer of the upper-level taxa. Primates as a whole are recovered well, as are the strepsirrhini, platyrrhini, and cercopithecids as monophyletic groups, while hominoids are not. This indicates that the hand is a region useful for elucidating relationships between all primates that are not hominoids, as all clades of monkeys are effectively recovered through use of these characters. Pectoral characters, on the other hand, separate cercopithecids, platyrrhini, and hominoids effectively and effectively recovering relationship but that of *Pongo* within hominoids. This indicates that the characters of the pectoral region are particularly useful when examining the relationships between great apes, and possibly useful in the reconstruction of fossil great ape relationships as well.

For a discussion of the synapomorphies and apomorphies driving the cladistic analyses, see the character definitions at the end of this work (Appendix 1) and discussion in Diogo and Wood (2011). They have already been discussed in that work, and so will not be repeated verbatim here.

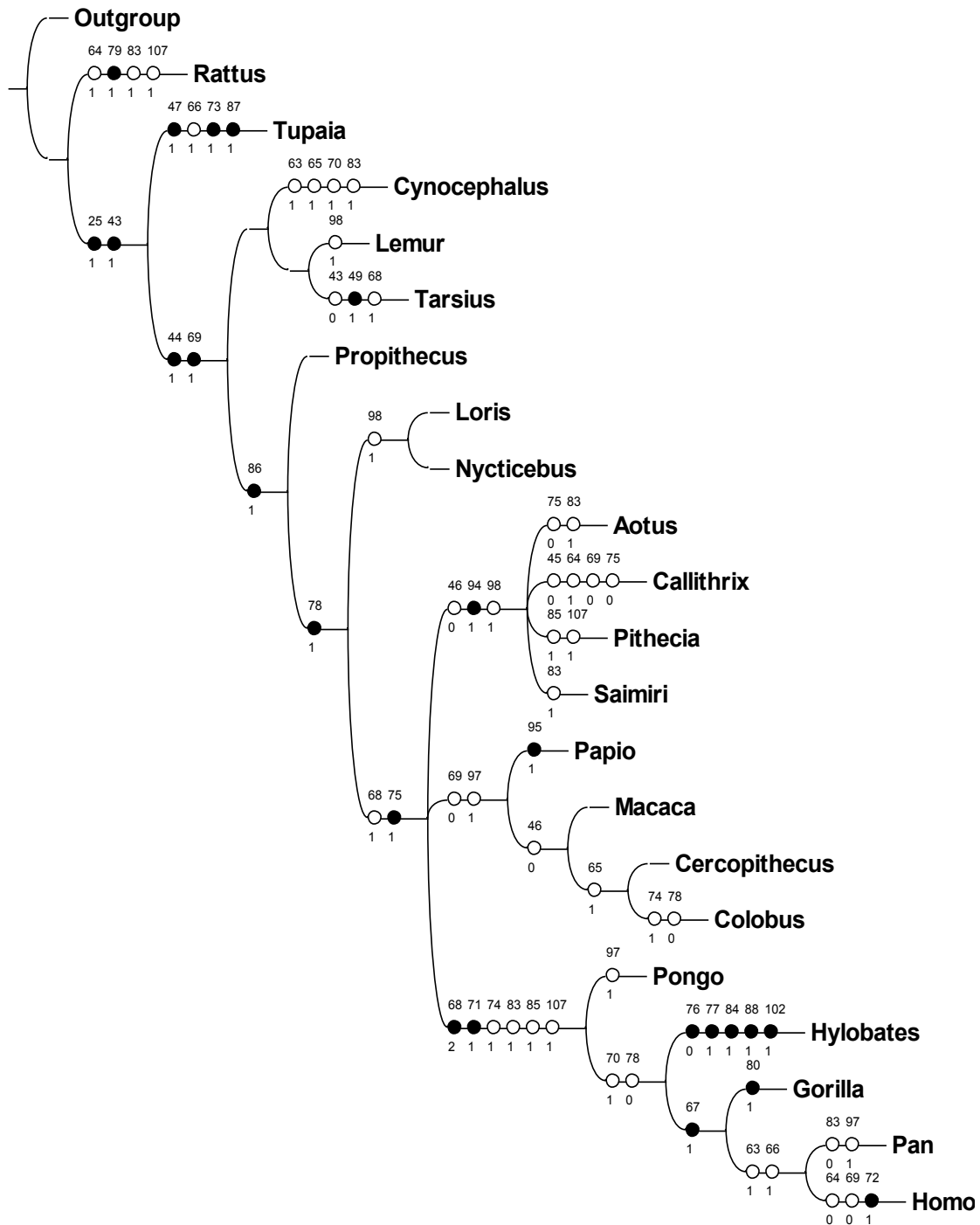


Figure 5: Pectoral consensus tree. From 43 most parsimonious trees (L:69, Ci:55, Ri:72). Unambiguous homoplasic (open dot) and non-homoplasic (black dot) character state changes are shown along branches. 9 of 19 clades correctly recovered (47.4%), Hominiini, Hominiinae, Hominoidea, Cercopithecidae, Platyrrhini, Anthroipoidea, Lorisiformes, Primatomorpha and Euarchonta. The only clades shown above not represented in 100% of the most parsimonious trees are the clade including *Cynocephalus*, *Lemur*, and *Tarsius* (67%), the *Lemur* and *Tarsius* clade (67%), the clade occurring at the branching of, and including, *Propithecus* (67%), Lorisiformes (88%), Cercopithecidae (97%), the *Macaca*, *Cercopithecus*, and *Colobus* clade (86%), Anthroipoidea (65%), and Platyrrhini (55%).

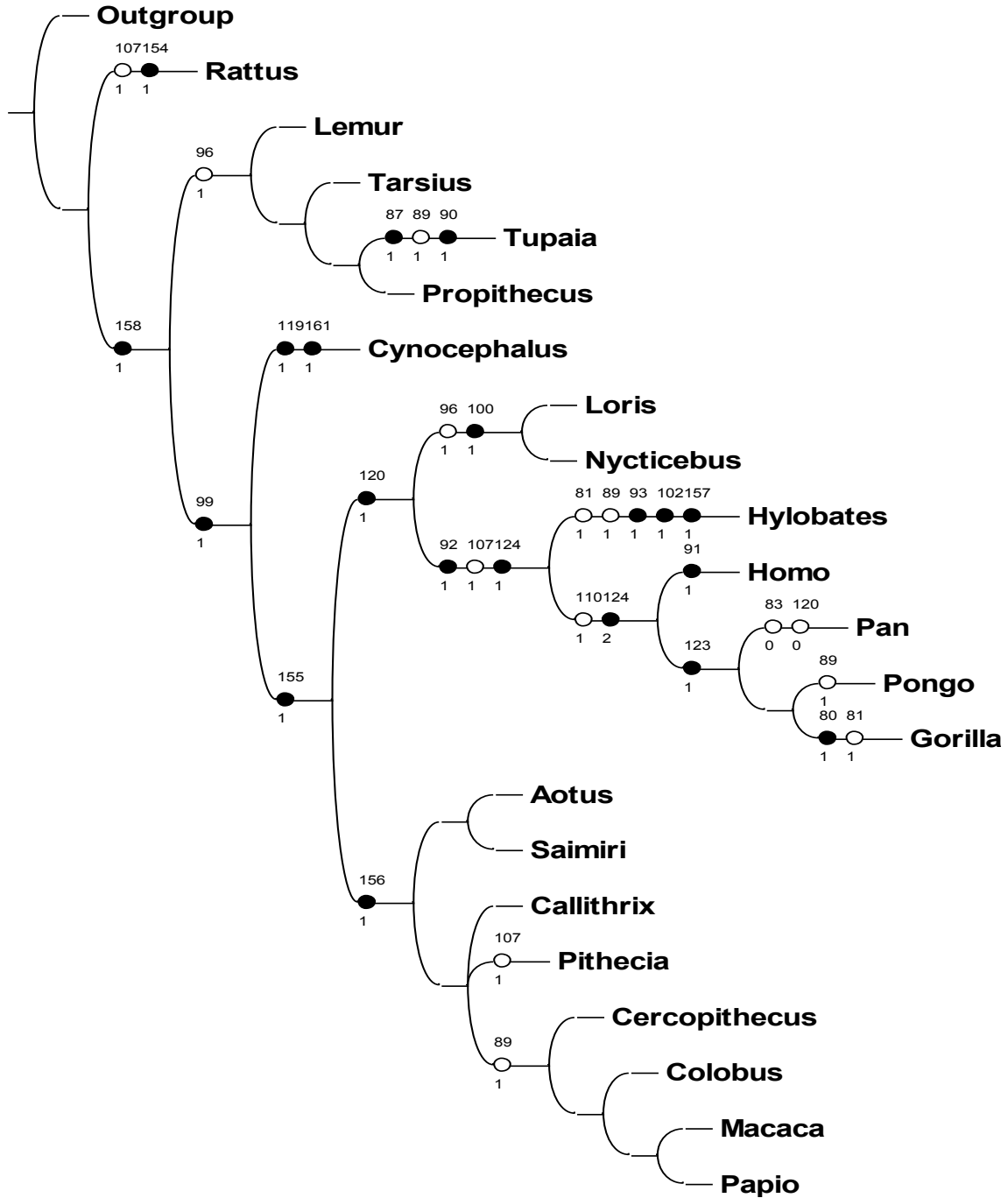


Figure 6: Arm consensus tree. From 4 most parsimonious trees (L:39, Ci:66, Ri:88). Unambiguous homoplasic (open dot) and non-homoplasic (black dot) character state changes are shown along branches. 6 of 19 clades correctly recovered (31.6%), Hominoidea, Hominoidea, Papionini, Cercopithecidae, Lorisiformes and Euarchonta. The only clades shown above not represented in 100% of the most parsimonious trees are the clade including everything except *Rattus* (75%), the *Aotus* and *Saimiri* clade (75%), and the clade including Cercopithecidae, *Callithrix* and *Pithecia* (75%).

Discussion

As the results of the cladistic analyses clearly indicate, such analyses are the most robust, and therefore the most accurate, when including the largest amount of information available, as demonstrated by the accuracy of the full dataset from Diogo (2011) compared to any of those done here. No regional phylogeny is as supportive of the available molecular, hard tissue, or soft tissue cladistics as the analysis driven by the entire dataset. Interestingly, the cladistic analysis that was predicted to be the most effective based on the amount of homoplasy in that region seen using the entire dataset, the pectoral region, was not the most effective region in recovering clades within primates. The hand region was more effective, which may indicate that instances of homoplasy seen in this region when examining the entire dataset appear as such to minimize actual homoplastic changes in other regions (i.e. actually homoplasies in pectoral and arm regions may result in a cladogram that uses those changes as homology and in turn takes a character change that is actually homologous in the hand region and uses it as a homoplasy to minimize the steps in or length of the tree). The number of homoplastic changes have not been calculated for the cranial region due to the reassignment of these characters for the present analysis.

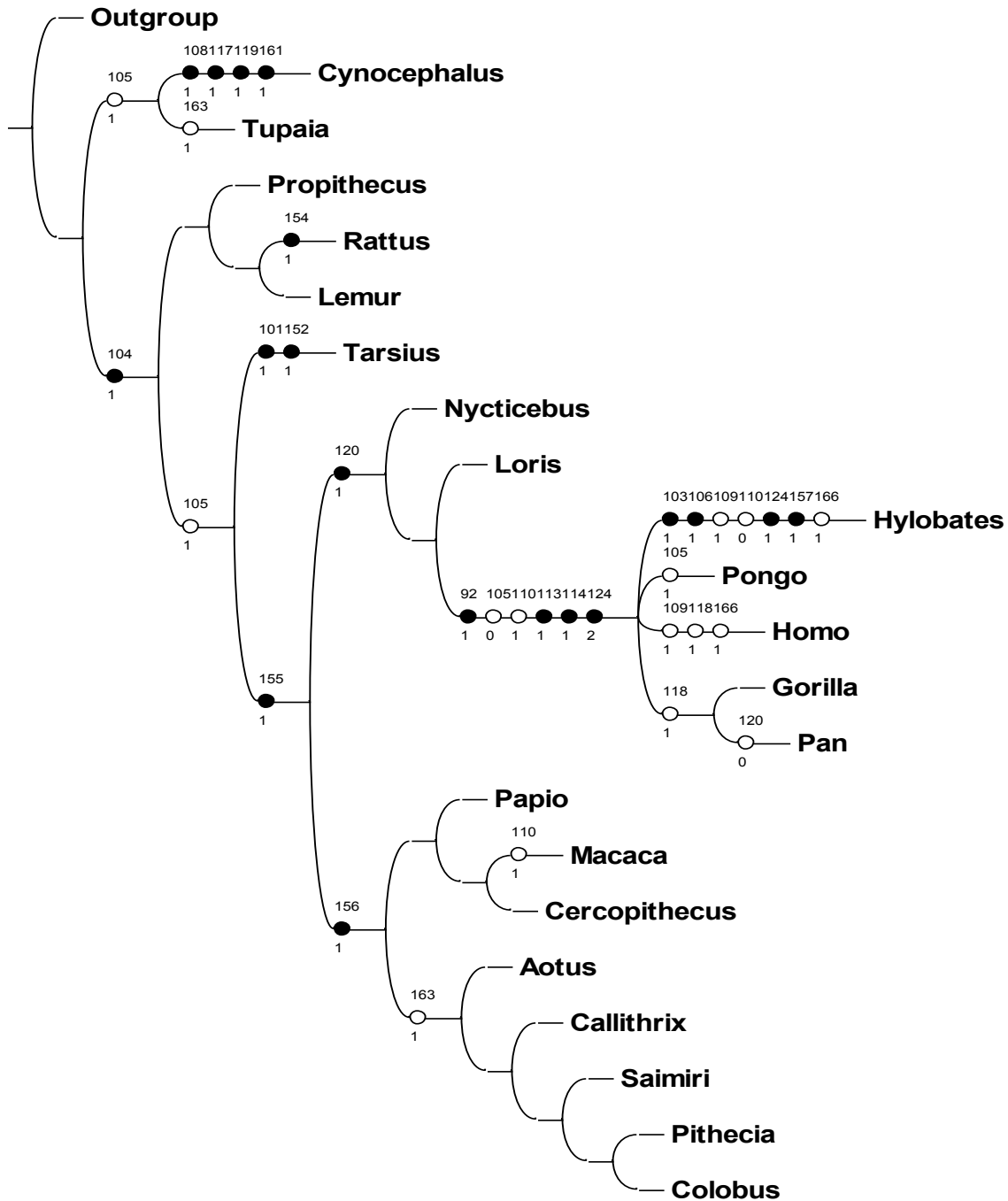


Figure 7: Forearm consensus tree. From 24 most parsimonious trees (L:39, Ci:66, Ri:78). Unambiguous homoplastic (open dot) and non-homoplastic (black dot) character state changes are shown along branches. 2 of 19 clades correctly recovered (10.5%), Hominoidea and Cercopitheciinae. The only clades shown above not represented in 100% of the most parsimonious trees are *Cynocephalus* and *Tupaia* (66%), *Propithecus*, *Rattus*, and *Lemur* (83%), *Rattus* and *Lemur* (83%), the clade occurring the branching of, and including, *Tarsius* (66%), and the *Gorilla* and *Pan* clade (75%).

These results do indicate that the cranial, hand, mandible, hyoid, arm and pectoral regions are all effective at reconstructing relationships within the primate order. All require relatively few (>5) characters on average to correctly recover one of the clades of interest for this study. In addition to recovering the most correct clades, the cranial region was also the most efficient at recovery, requiring on average fewer characters than any other region. This may be due to the increased value of additional character data in phylogenetics, which again argues for the largest amount of data available to be utilized, but also implies that this region is of the most use for fossil reconstructions. This is promising in that many studies of fossil Hominina members already proceed using a lot of data from this region. The hyoid region was also quite efficient at recovery of primate clades. Hyoid bones are rarely found in fossilized form, and so their use to the study of human origins in this manner is somewhat diminished. Where hyoid bones are available, however, this study indicates that they are invaluable sources of information pertinent to the relationships of these fossil taxa. Mandibular characteristics proved almost as efficient as hyoid characters, and so mandibles should also be preferentially used when available. Bones of the pectoral region, the humerus, bones of the hand and wrist are also acceptably efficient at recovering relationships between primate taxa, and should be used where available. While the radius and ulna provide somewhat less efficient means of recovery, they still provide important sources of information. The results do indicate, however, that it may be prudent to avoid the forearm bones in analyses where other body regions are available for study, as their recovery rate and efficiency are quite worse than any of the other regions.

It must be noted that, while the homoplasy trends in the original cladistic analysis did not correctly predict the pectoral region's usefulness as a dataset for primates as a

whole, there was indeed a low level of homoplasy within hominoids specifically in this region (5 non-homoplastic changes and one homoplastic change). That prediction seems to hold true for that clade, as it recovers all of the relationships except one. The cranial and hyoid regions also correctly reconstruct relationships within the hominoid clade. All three effectively recover most of the relationships largely supported through larger-scale cladistic analyses at this level using both morphological and molecular information (Shoshani et al., 1996; Diogo and Wood, 2011). Therefore, this analysis lends support to those clades, and implies idea that the cranial, pectoral, and hyoid regions should be further investigate for more intense cladistic analyses of the Hominoidea.

In addition, none of the seven analyses resulted in a grouping of humans and *Pongo*, which is argued for by some authors and critics of the molecular studies (Schwartz and Maresca, 2006). Indeed, it makes it seem as though recovering such a clade would be difficult using myological characters from the upper body of primates in light of the present study. These data do not support such a clade when taken as a whole, or when examined as any of seven different subsets, implying that these characters in no way could support such a relationship. The myological data therefore not only support the (*Pan – Homo*) clade, but argue strongly against the (*Pongo – Homo*) clade.

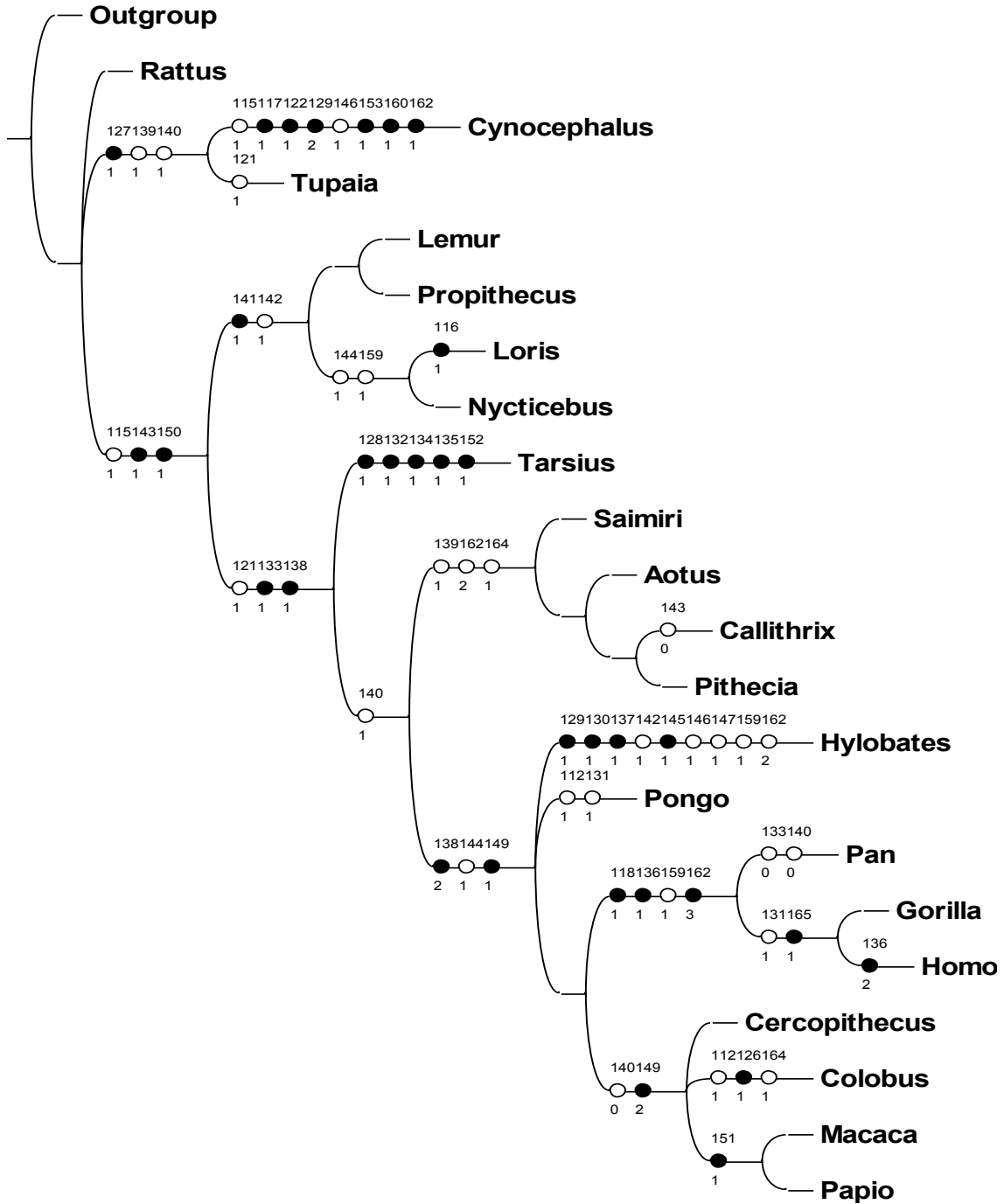


Figure 8: Hand consensus tree. From 34 most parsimonious trees (L:71, Ci:67, Ri:78). Unambiguous homoplastic (open dot) and non-homoplastic (black dot) character state changes are shown along branches. 10 of 19 clades are correctly recovered (52.6%), Hominae, Papionini, Cercopithecinae, Catarrhini, Platyrrhini, Anthropoidea, Haplorrhini, Lorisiformes, Lemuriformes, and Primates. The only clades shown above not represented in 100% of the most parsimonious trees are Platyrrhini and *Tarsius* (52%), Cebidae and Aotidae (88%), and Cercopithecidae (52%).

Chapter 3: Macroscopic Recovery of Myology in the Human Skeleton

Background

Recovery of the soft tissue characters used for the first section of this study from hard tissues would be invaluable to the field of primate paleobiology. Definitive proof of muscle attachment sites would allow researchers to begin to systematically reconstruct the myological anatomy of extinct species through the use of direct evidence of these muscles. Though some reconstruction has been used in this field, the evidence upon which it is based is quite indirect (Strait et al., 2005). Given the nature of the interaction between muscle, especially skeletal muscle, and the underlying hard tissue, such a reconstruction is not illogical (Gross et al., 2010; Hamrick et al., 2010; Nowlan et al., 2010; Qin et al., 2010). Such interactions can result in both macroscopic and microscopic changes to the structure of the skeletal bone, which support the assumptions of those indirect reconstructions (Benjamin et al., 2002; Syropoulos, 2005; Bayrum et al., 2009). However, instead of assuming increased muscle mass based on other traits of a presumed adaptive suite, having direct evidence would allow researchers to discern the muscle characters themselves and in turn use that to further strengthen arguments about the existence of said adaptive suite of characters.

Reconstruction of muscle from skeletal characters has been attempted before. Many of these attempts are examining the relationship between muscle and skeletal structure in birds and other reptiles, and attempting to reconstruct these characters in fossil dinosaur species (see Suzuki et al., 2002; Suzuki, 2003). Most work acknowledges the gap between discovering the effects of muscle presence and action on bone and application of

this evidence to fossil studies. This has been done macroscopically in non-primate mammals as well (Bryant and Seymour, 1990). Here, we attempt to add to the body of knowledge that is of use for direct reconstructions of myology in the human lineage. Because of the limitations of the available material and methods, this study examines the aforementioned macroscopic relationships between muscle and bone to provide a first, non-destructive step in direct muscle reconstruction in fossil Hominina species.

Methods

The 92 characters from Diogo and Wood (2011) designated as “possibly examined in fossils” (Fig. 9), those associated with hard tissues of the upper limb, pectoral, head and neck regions, were examined in human cadavers. Access and time constraints limited this examination to only those characters that were recoverable in modern humans. All characters were examined on cadavers at the Howard University College of Medicine. All dissections were performed on-site at the cadaver lab of the HUCM. Reference skeletal material was also provided by HUCM through the teaching specimens located in the aforementioned cadaver lab as well as in Dr. Rui Diogo’s lab in the anatomy department. The specific cadavers used were D45, M15, M10 and M08. These cadavers were supplied to the dental and medical students enrolled in the introductory gross anatomy labs. Because of this, my access was restricted to portions of the cadavers that had largely been dissected previously, and so the state of the bodies requires special note.

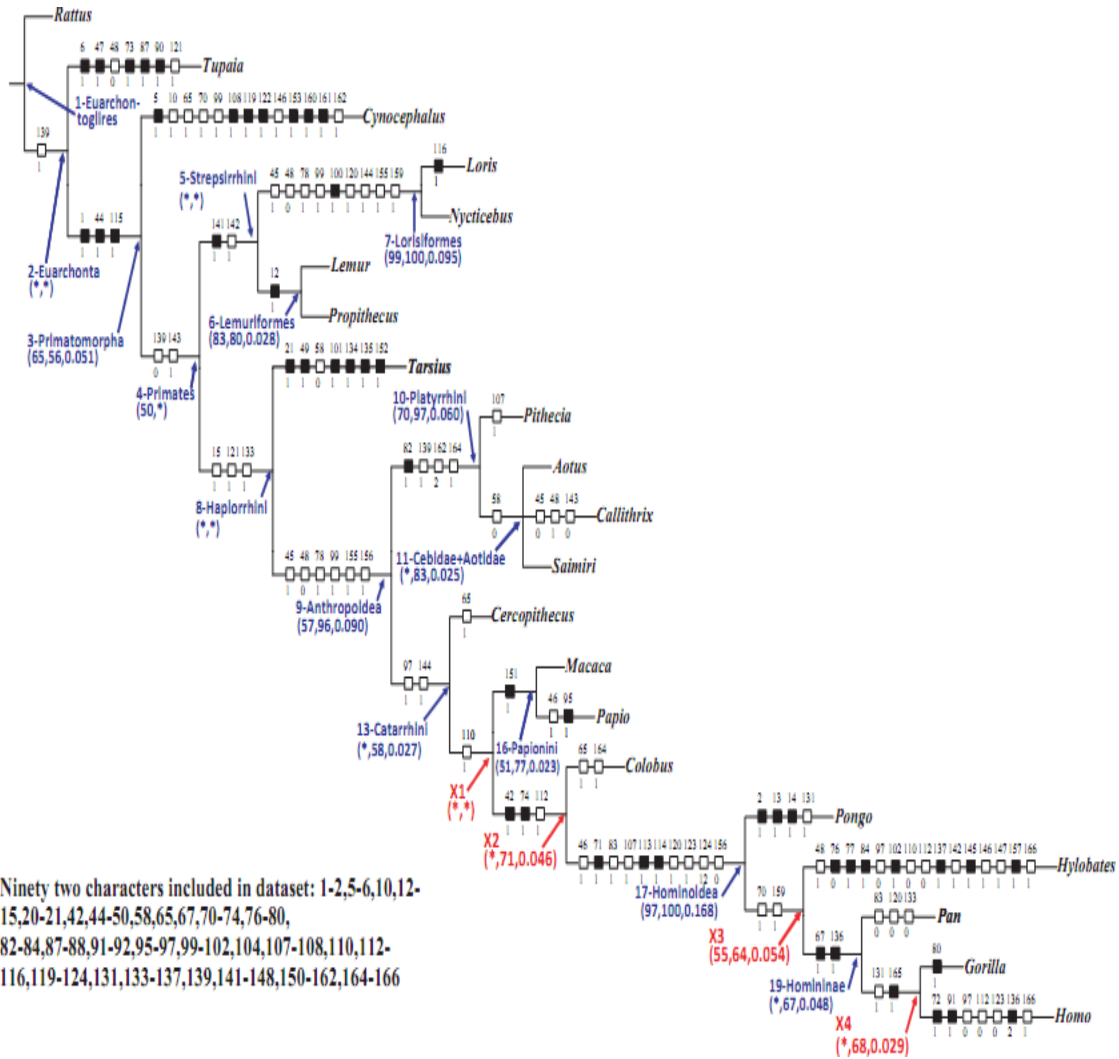


Figure 9: Cladistic analysis of the ninety-two characters by Diogo and Wood (2011) that could possibly be recovered in fossilized hard tissue. Unambiguous homoplastic (open dot) and non-homoplastic (black dot) character state changes are shown along branches. 14 of the 19 clades (those not denoted as an “X” clade) correctly recovered.

The specimens, though graciously offered and thankfully accepted, were oftentimes desiccated and both muscle and skeletal tissue were often damaged to the point where it was impossible to try and recover some characters. Several methods were used to try and minimize this impact. First, any named or widely-accepted bony correlate for the muscle characters was searched for in the literature (e.g. Gray, 1858; Netter, 2010) and popular anatomic references, as well as through an internet search to determine any common or

colloquial references to attachment sites. In some cases (i.e. most characters involving the *trapezius m.*), this was the only way to search for any bony correlate. Otherwise this literature search was used as a guide for the examination of the cadaver material, and to ensure accurate reference of individual, small scale bone structures. Second, several cadavers were used to search for the most intact example of any given character. This resulted in only obvious associations between a muscle and a skeletal character being taken as a recoverable character in fossil members of the subtribe Hominina. Though these are limitations to the present study, they ensure that only definitively recoverable characters are indeed recovered in this analysis.

Because of the use of only human specimens, only a certain amount of the characters examined in Diogo and Wood (2011) were possibly recoverable in this examination. Only characters in which the human state is “positive” were looked for. This means that the humans must possess the bony attachment in question for a given character to be searched for. For example, character #15 is the presence of the *jugulohyoideus m.*, which is not present in modern humans. Because of this, there will not be a bony attachment in humans, and so there is no point in searching for the lack of a bony attachment without some comparative non-human specimen that exhibits the positive state of this character (that the muscle is present and does have a bony correlate). Characters that state the attachment of a muscle to a certain structure or area of a structure can also fall into this category, such as #14 in which the *digastricus posterior m.* is directly attached to the mandible (which is not the case in modern humans and so cannot be searched for). By these criteria, 44 characters were suitable for examination in the human body; the

characters examined were 2, 6, 10, 12, 45-48³, 50, 58, 65, 67, 77, 78, 83, 87, 97, 99-102, 104, 108, 112-115, 121, 124, 136, 139, 143, 144, 148, 150, 153-158, 165 and 166.

The examination proceeded by finding the muscle of interest for a given character, and tracing it to its origin(s) and insertion(s). Attachments of interest were cleaned for a clear examination of the entire attachment site. If the character being examined was a change in an insertion or origin only, then only one of the attachments was of interest. If the character was the presence or absence of a muscle, then all attachment sites were examined for bony correlates. Once the entirety of the attachment site was exposed, the site was photographed, and the muscle was reflected at the attachment site. The bone was searched for any hard tissue structure, such as a tuberosity, groove, ridge, etc. that was unique to the area of attachment. If there was a structure that seemed to be associated with the attachment site, the area around this site was also cleaned off to ensure that the hard tissue structure was uniquely associated with the attachment of that muscle. For characters that did appear to have a correlate on one of the HUMC cadavers, the bony correlate was photographed, and then the reference skeletons were also examined for that bony landmark. If they had an identical or very similar bony landmark, the structure was accepted as an indication of the presence of that muscle attachment. Such a unique structure was deemed to be sufficient for recovery of the soft-tissue character from skeletal remains, and would indicate the presence of that muscle on a fossil human. If the attachment site was not unique to the muscle (i.e. attachment of the common flexor tendon on the humerus), it was not taken as a bone correlate. No method for quantifying how different the skeletal

³ Bodies were too damaged, so these characters were only examined through the literature.

attachment site of a muscle is to the surround skeletal tissue exists, and so this examination was necessarily qualitative.

The recoverable characters (23 in total, characters # 2, 10, 12, 48, 58, 65, 78, 87, 97, 104, 108, 112, 114, 121, 143, 144, 148, 150, 153, 154, 155, 157 and 165; see below) were then used in a cladistic analysis. Analyzing these characters in this manner can help determine whether such resolution is of use for the phylogenetic study of fossil human ancestors and apes. Methods for this cladistic analysis were the same as the above section.

Results

As previously mentioned, of the myological characters examined by Diogo and Wood (2011) possibly recoverable in hard tissue, only 23 are definitively recoverable from a macroscopic examination. Each character is associated with a unique skeletal structure in a cadaver, and this structure is present in the reference skeletons as well. The skeletal structure for each of the recoverable characters is described here. Characters are presented by region for the above phylogenetic analyses, but explanations below only appear for one of these regions when a character has been used for multiple analyses.

Pectoral Region

#65 “*Omohyoideus is not a distinct muscle*”. This character refers to the existence of the *omohyoideus m.*, which exists in modern humans. The muscle attaches to the scapula and the inferior portion of the hyoid bone. A very minor depression was found on the scapula at the site of attachment, but this was not taken as a definitive enough character to be a bone correlate for this character. However, a small distinct tubercle was found on

the antero-inferior, lateral portion of the basion of the hyoid, and was taken to be a bony correlate of this character.

#78 “*Pectoralis major has no clavicular origin*”. This character refers to the presence of a clavicular origin of the *pectoralis major m.*, which is present in modern humans. No named region for this attachment site was found in the literature. However, a distinct, shallow groove was found on the clavicle uniquely associated with the area of attachment of this muscle.

#87 “*Teres minor is not a distinct muscle*”. This character refers to the existence of the *teres minor m.*, which modern humans possess. The literature refers to the attachment site as flat impression of the greater tubercle on the humerus (Gray, 1858) and/or the inferior facet of the same region. A unique association was found between the insertion of this muscle on the humerus and a small circular tuberosity as well as the raised “v”-shaped area immediately inferior to this tuberosity on the postero-lateral side of the humerus and extending on to the head of the bone.

#97 “*Long head of the triceps brachii originates from half or more than half of the lateral border of the scapula*”. This character refers to the length of attachment of the *triceps brachii m.* on the scapula, which in modern humans is longer than in some of the other taxa (i.e. it is a positive positional change realized in humans that can be searched for). In some of the literature sources this attachment is unnamed, but in others it is referred to as the infraglenoid tuberosity (Gray, 1858). The attachment of the *triceps brachii m.* on the scapula is uniquely associated as with a thicker portion of the inferior border of the scapula in the cadavers examined for this project.

Arm Region

No definitive bony correlates were found at muscle attachment sites on the humerus.

Forearm Region

#104 “*Biceps brachii does not insert onto the ulna*”. This character refers to the *biceps brachii m.* insertion on the ulna, which it does in modern humans. Often, the literature attributes this insertion to the radial tuberosity of the ulna, which is what this work found as well (Gray, 1858; Netter, 2010). More specifically, this work found that the insertion of this muscle on the ulna corresponds to the deep groove or pit of the radial tuberosity on the ulna.

#108 “*Pronator quadratus is not a distinct muscle*”. This character refers to the existence of the *pronator quadratus m.*, which exists in modern humans. Sources in the literature refer to the origin as the “pronator ridge” (Gray, 1858), while the insertion is referred to as a triangular area or, alternatively, the “pronator fossa” of the radius (Gray, 1858; Nelson, 2010). This work found a more definitive unique structure associated with the origin on the ulna, which does indeed correspond to the pronator ridge, but also the flat and rough area around the ridge. The insertion is associated with a similar, but less severe, structure on the radius.

#114 “*Flexor digitorum superficialis originates from the ulna*”. This character refers to whether the *flexor digitorum superficialis m.* attaches to the ulna, which it does in modern humans. This attachment site is referred to as the “medial aspect of the coronoid process” (Gray, 1858; Jenkins, 2009), as well as the “medial border of the coronoid process

and fibrous arch” (McNulty and Dauzvardis, 2011). This work found this ulnar origin to be definitively associated with a sharp ridge on the non-radial side of the ulna and most palmar aspects of the coronoid process.

#154 “*Brachioradialis is not a distinct muscle*”. This character refers to the existence of a *brachioradialis m.*, which exists in modern humans. The literature is described as the lateral supracondylar ridge in several sources, none of which give a distinct name for this attachment site, however (Gray, 1858; Jenkins, 2009; Wheelless et al., 2011; McNulty and Dauzvardis, 2011). The origin is unnamed. This work found that the insertion is clearly associated with the supracondylar ridge and the raised rough patch at the very distal, non-ulnar region near this ridge. The origin is associated and outlined by ridges on the lateral and medial side of the humerus, but this is not nearly as definitive a bone correlate as the insertion.

#155 “*Supinator has no ulnar head*”. This character refers to the existence of the ulnar head of the *supinator m.*, which modern humans possess. Only the origin of the muscle will be affected by this character, and the literature refers to the attachment site as the “supinator crest” of the ulna (Wheelless et al., 2011; McNulty and Dauzvardis, 2011). This work found that the supinator crest was in fact the unique structure associated with this character, and was taken as the hard-tissue correlate.

#157 “*Anconeus is not a distinct muscle*”. This character refers to the existence of the *anconeus m.*, which exists in modern humans. Only the general attachment sites are described in the literature, such as the origin on the lateral epicondyle of the humerus and the lateral side of the olecranon process of the ulna (Gray, 1858; Richardson, 1997; Jenkins, 2009; Netter, 2010; Wheelless et al., 2011). This work found that the origin is

definitively associated with the bottom of the medial ridge on the lateral epicondyle, while the insertion is definitively associated with the ridge on the olecranon process.

#165 “*Abductor pollicis longus extends to the proximal phalanx of the thumb*”. This character refers to the more distal insertion of the *abductor pollicis longus m.*, which occurs in modern humans. The attachment is unnamed in the literature. This work found a definitive association between the insertion of this muscle on the posterior side at the base of the proximal phalanx of the thumb in the form of a small tubercle. Character 166 is deemed unrecoverable because this bony correlate should also be found in gorillas, which possess an extension of this muscle, but do not have the *extensor pollicis brevis m.* referred to by character 166.

Hand Region

#112 “*Tendon of flexor digitorum profundus to digit 1 is vestigial or absent*”. This character refers to whether the tendon of the *flexor digitorum profundus m.* extends to the first digit or not, which it does in modern humans. None of the literature described this insertion site. The attachment site of this tendon on the is associated with the raised “platform” NOT immediately distal to the joint, but approximately 1/3rd the length of the distal phalanx away from this joint. Susman (1994) argues that this landmark can also indicate the presence of the *flexor pollicis longus m.* in modern humans, but as that was not included in the original 92 character dataset it is not taken as a recoverable character here. It should be examined in future studies.

#121 “*Flexor carpi radialis inserts onto the metacarpals II and III*”. This character refers to the attachment of the *flexor carpi radialis m.* on the second and third metacarpals,

which modern humans possess. In the literature, this is described as the base of these metacarpals, as well as occasionally the “trapezial tuberosity” (Gray, 2858; Jenkins, 2009; Netter, 2010; Wheelless et al., 2011). This work found a similar structure associated with this attachment, as there is a smooth, raised area at the base of each metacarpal on the trapezial side where these tendons attach.

#143 “*Opponens pollicis is a distinct muscle*” and #144 “*opponens pollicis reaches the distal portion of metacarpal I*”. These characters refer to the existence of the *opponens pollicis m.*, which modern humans possess, as well as the insertion of the muscle on the distal portion of the metacarpal I, which it does in modern humans as well. Literature often does not name the attachment sites of this muscle, but occasionally refers to the origin as the “flexor retinaculum and tubercle of trapezium bone” (Richardson, 1997; Wheelless et al., 2011). In this work, the origin was associated with the above structures, but they were not taken to be uniquely due to this muscle as there are so many attachments within this portion of the wrist. However, the insertion was uniquely and definitively associated with the whole length of the lateral ridge of the proximal phalanx of the thumb.

#148 “*Opponens digiti minimi is a distinct muscle*” and #150 “*Insertion of opponens digiti minimi extends proximally to the distal part of metacarpal V*”. These characters refer to the existence of the *opponens digiti minimi m.* and its subsequent proximal attachment on the fifth metacarpal, which both exist in modern humans. The literature refers to the origin of this muscle as the “convexity of the hamulus of the hamate bone” (Gray, 1858), or the “hook of the hamate” (Richardson, 1997; Jenkins, 2009; McNulty and Dauzvardis, 2011; Wheelless et al., 2011). Because of the other complicated relationships this structure has with other soft-tissues, it was not taken to be a definitive

indication of the muscle's existence. However, the insertion was definitively associated with ridges along the length of the palmar/lateral side of the fifth metacarpal, which clearly border the attachment site.

#153 "*Extensor carpi radialis longus does not insert onto the metacarpal II*". This character refers to the insertion of the *extensor carpi radialis longus m.* on the base of metacarpal II in modern humans. The literature does not name the attachment site, except for as the "base" of the metacarpal in common online sources (Gray, 2858; Jenkins, 2009; Netter, 2010; Wheelless et al., 2011). Attachment of this muscle on the metacarpal was associated with a definitive, raised facet oriented slightly proximally on the base of the second metacarpal.

Cranial Region

#48 "*Trapezius does not originate from the cranium*". This character refers to the origin of the *trapezius m.* from the occipital bone of the cranium, which exists in modern humans. The tubercles of the bottom of the external occipital protuberance were associated with this attachment site in the human body, and are taken as the bone correlate of this character.

Mandibular Region

#2 "*Digastricus anterior is not a distinct muscle*". This character refers to the existence of the anterior belly of the *digastricus m.*, which exists in modern humans. This work found a definitive small tubercle and rough patch outlining the insertion of this muscle on the medial side of the chin on the mandible.

Hyoid Region

#10 “*Stylohyoideus is not a distinct muscle*” and #12 “*stylohyoideus is inserted near the midline*”. These characters refer to the existence of the *stylohyoid m.* and its subsequent attachment near the midline on the hyoid bone, both of which exists in modern humans. Though this muscle originates from the styloid process, other things attach to that structure and so it is not taken to be a definitive correlate of this character. However, a small depression on the anterior basion/lesser horn of the hyoid was found to be definitively and uniquely associated with the attachment site of this muscle.

#58 “*Chondroglossus is present as a distinct bundle of the hyoglossus*”. This character refers to the existence of a belly of the *hyoglossus m.* attaching to the greater horn of the hyoid bone, which exists in modern humans. A definitive, slight depression on the greater horn of the hyoid bone was correlated with this attachment. In addition, the hyoid bone thins immediately lateral to the attachment of this muscle.

Phylogenetic Analysis

As previously stated, a phylogenetic analysis was performed on the 23 macroscopically recovered characters. The consensus majority tree generated from these characters provides a cladogram that does correctly recover six of the clades of interest (31.6%), at an efficiency rate of 3.83 characters required per clade recovered. Importantly for this, modern humans and chimpanzees do not appear as sister groups in this analysis. However, as discussed below, these reconstructions could in fact be promising for elucidating the relationships between possible fossil Hominina species.

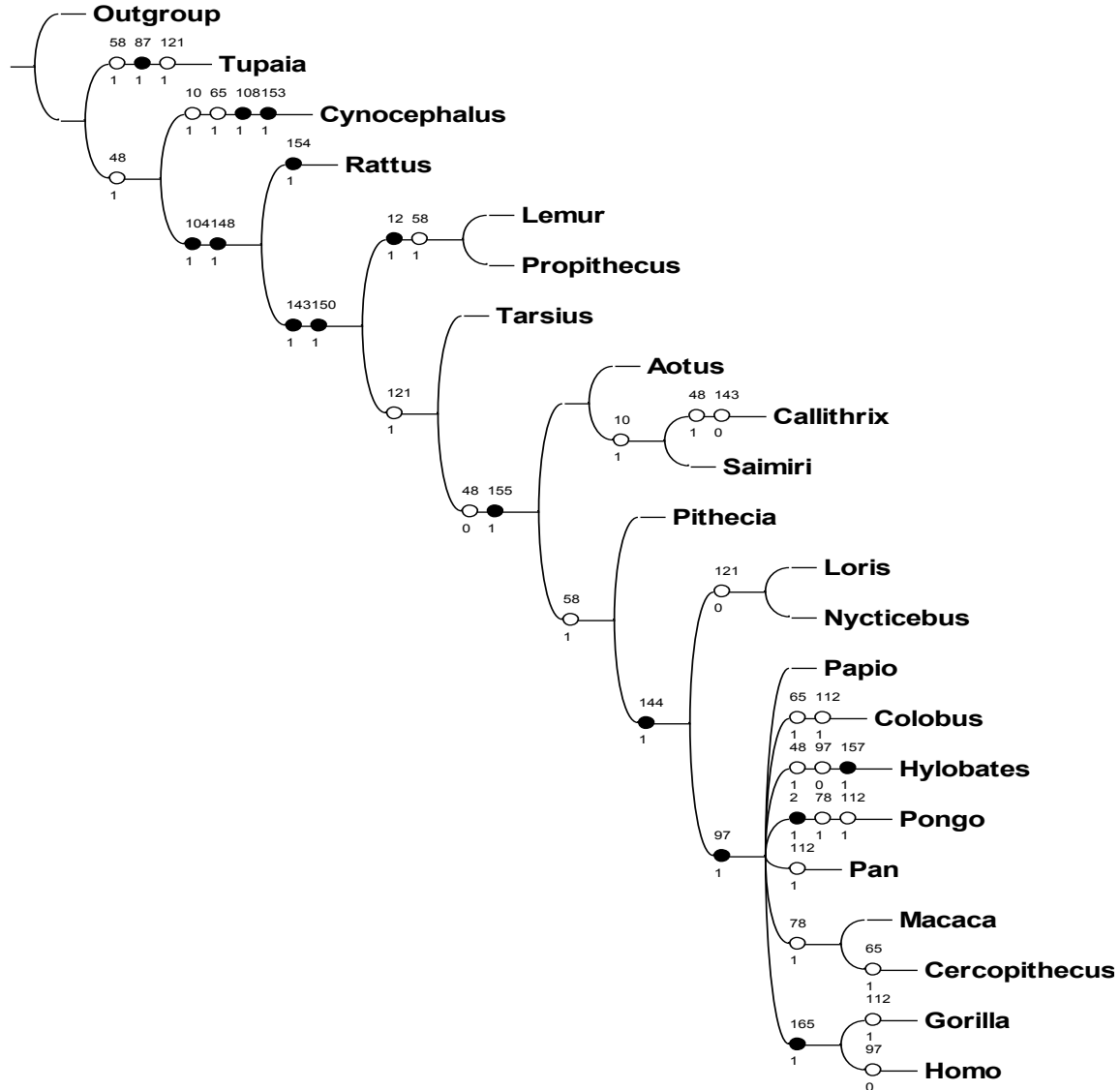


Figure 10: Consensus majority tree generated from the 23 characters macroscopically recoverable in skeletal material. From 105 more parsimonious trees (L:41, Ci:56, Ri:70). Unambiguous homoplastic (open dot) and non-homoplastic (black dot) character state changes are shown along branches. 6 of 19 clades correctly recovered (31.6%), Catarrhini, Cebidae, Aotidae+Cebidae, Lemuriformes, Lorisiformes and Primates. The only clades shown above not represented in 100% of the most parsimonious trees are *Macaca* and *Cercopithecus* (66%), *Gorilla* and *Homo* (54%), Catarrhini (70%), Catarrhini+Lorisiformes (85%), Catarrhini+Lorisiformes+*Pithecia* (85%), Cebidae (62%), Aotidae+Cebidae (62%), Anthrooidea+Lorisiformes (94%), and Haplorrhini+Lorisiformes (91%). The “wrong” relationship between *Homo* and *Hylobates* is recovered in 100% of the trees using these data, likely because of the highly derived nature of the hands of both taxa.

Discussion

Though the results of this analysis have proven less than ideal in terms of the number of overall characters that have been recovered here, it shows that recovery of these characters is possible and comparable to those previously done for other taxa. Of the 92 theoretically recoverable characters, only 23 had definitive macroscopic correlates on the associated bone at attachment sites (25%). This is within the range of the studies of Brown kiwi bird musculature and those of *Canis* and *Ursus* specimens (McGowan, 1979; 1982; Bryant and Seymour 1990). While this means that researchers trying to reconstruct these relationships from macroscopic evidence are missing approximately 3/4 of the information, it does indicate how fruitful more in depth studies of these relationships could be, particularly if using complementary techniques such as histology and microscopy. Moreover, there are several important differences between this study and those done previously that may result in a lower recovery rate in the present analysis than truly possible. For example, while Bryant and Seymour (1990) examined whether individual muscle attachment sites could be recovered from the osteology of the animal, this study used some characters that do not necessarily have a unique, unshared attachment site. For example, forearm muscles (ontogenetically speaking) that originate with each other from the common flexor tendon were used in this analysis, while it is highly unlikely that similar attachments were examined by Bryant and Seymour (1990). Attachment of multiple muscles to one bony landmark makes relating a macroscopic bony correlate to an individual muscle impossible. Narrowing the set of characters being examined to only those that would fit the criteria of these previous studies would increase the proportion recoverable.

As explained above, the value of recovery efforts of muscle tissue from skeletal tissue could also be further improved by a more complete primate sample and greater methodological variety. For instance, examining non-human primates would provide contrasts for comparative analysis of attachment sites at the macroscopic level, to provide more conclusive evidence that the bony landmarks recovered in this analysis were uniquely due to the attachment of the associated muscle. Likewise, such a sample would allow the possible recovery of characters that are not even present in the modern human body (such as character #15, the presence of the *jugulohyoideus m.*, the attachment site of which cannot be examined in humans as the muscle is not present in our species). Additional methodological approaches would also, theoretically, improve the proportion of these soft-tissue characters that are recoverable in skeletal material, while also providing further support for those characters already recovered macroscopically. Histological sectioning and examination of Sharpey's fibers, as well as SEM examination of surface morphology of the attachment sites would be valuable in this way (Benjamin et al., 2002; Hieronymus, 2006).

Having 23 of these characters is surprisingly valuable to the study of primate relationships. Six of the 19 accepted clades are recovered from only these few characters, which is quite impressive for such a small dataset. In fact, this dataset has a recovery rate of 3.83 characters per clade recovered, making it more efficient at recovering these relationships than more than half of the regional datasets. These characters effectively elucidate the catarrhine clade and do not group tarsiers in a monophyletic group with the strepsirrhini (though it does this by grouping Lorisiformes in a monophyletic group with the catarrhines). Much like the recovery patterns in the entire ninety-two character dataset

of Diogo and Wood (2011), this analysis is worst at recovering relationships within the catarrhines, and better at recovering relationships outside of that group (in fact, the misplacement of Lorisiformes and *Pithecia* are the only 2 inaccurate relationships within primates, outside of catarrhines). In addition, these results indicate which regions should be the most informative to the discussion of human evolution with regard to the fossil record. As evidenced by many studies, our closest living relatives are chimpanzees, including common chimpanzees and bonobos (Shoshani et al., 1996; Steiper and Young, 2006; Fabre et al., 2009; Arnold et al., 2010). Therefore, it is those characters in which differences between modern humans and chimpanzees exist that are likely the most important for parsing out relationships between fossil members of our Hominina subtribe, especially the most plesiomorphic members of this subtribe. The above results indicate that the characters recoverable in fossil material group humans and chimpanzees quite disparately. Initially what seems like a shortcoming of the analysis may actually indicate that these characters are useful specifically for examining the ancestors of humans and chimpanzees, as they clearly differentiate between the two. Moreover, the results indicate the presence of multiple instances of homoplasy with other primate species (especially *Hylobates*) in the characters recoverable in skeletal material; this could obfuscate the examination of these characters within the fossil record of the Hominoidea, but also provide an opportunity to elucidate valuable information about the homoplasy and evolution of this superfamily if studied carefully.

Only four of the characters examined are both recoverable in skeletal material and found in different states in chimpanzees and humans, with two of these found in the forearm bones. However, it is likely that even those muscles that do not attach directly to

skeletal bone do affect the underlying bone in some way (or, alternatively, represent changes in this underlying bone). Of the 166 characters in the full dataset, five characters exhibit state differences between the two species in both the hand and arm regions. The inclusion of chimpanzee specimens in the sample study, as well as the use of other methods to find attachment sites in skeletal material would likely recover more of these 166 characters, and likely change the pattern to match that seen in the overall data. Because of this, the humerus and hand bones are likely the best skeletal regions to look for differences between Hominina species when determining phylogenetic relationships.

Obviously a significant drawback is the fact that this study draws information from the complete upper skeleton, which is rarely available for fossil species. One should also note, however, that this means the majority of the muscles of the body are not being included in this analysis, and can and should be included in future studies. Overall, the present study gives an indication of how valuable this data will be when a more intense recovery effort (or series of efforts) is used.

The above results are somewhat limited in the type of information they can provide to a soft-tissue reconstruction. Unlike some past attempts at soft-tissue reconstruction from skeletal material, the present study only sought to elucidate the presence of a given muscle or the placement of its attachment site, as opposed to the size or action of the muscle (Benjamin et al., 2002). Thus, the reconstructions possible through these results would not indicate how functionally important a muscle is in terms of loading, directionality, or mass. The study does, however, provide exciting information on the presence and position of muscle attachments from bony correlates, both of which are invaluable to both phylogenetic and functional reconstructions. Such information can obviously be coded for

phylogenetics, as has been done here and previously. The ability to directly evidence the existence or position of a muscle is often enough to infer the function of that muscle as well. This allows soft tissue information to be used in arguments about a species' activities, and strengthen arguments about its ecological niche. Further examination of the relationship between these muscle attachment sites and skeletal material will provide more specific information about how to directly evidence muscle characteristics from bone, and allow for a more complete understanding of the fossil record.

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Appendix I. List of the original 166 characters from Diogo and Wood (2012)

* This brief summary of the list of the 166 phylogenetic characters used by Diogo and Wood (2011b) is divided into the original nine ontogenetic subgroups of muscles used by those authors.

Mandibular muscles

1. *Intermandibularis anterior* is not a distinct muscle. Contrary to taxa of CS-0 [0], in *Cynocephalus* and the primates included in this study [1] there is usually no fleshy, separate intermandibularis anterior.
2. *Digastricus anterior* is not a distinct muscle (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Pongo* [1] the digastricus anterior is usually not present as a distinct muscle.
3. *Digastricus anterior* is not in contact with its counterpart for most of its length. Contrary to taxa of CS-0 [0], in *Cynocephalus*, *Lemur*, *Propithecus*, *Loris*, *Nycticebus*, *Aotus*, *Callithrix*, *Pithecia*, *Colobus*, *Cercopithecus*, *Hylobates* and *Homo* [1] the digastricus anterior does not contact its counterpart for most of its length. [-] Inapplicable in *Pongo*, because the digastricus anterior is usually not present as a distinct muscle.
4. *Digastricus anterior* is not connected to the *digastricus posterior* by a well-defined intermediate tendon (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Cynocephalus* [1] the digastricus anterior and digastricus posterior are not connected by a well-defined tendon, but instead by a short muscular intersection. [-] Inapplicable in *Pongo*, because the digastricus anterior is usually not present as a distinct muscle.
5. *Digastricus anterior* attaches onto the angle of the mandible (AUTAPOMORPHY). Contrary to taxa of CS-0 (in which the digastricus anterior usually inserts onto and/or near the mandibular symphysis) [0], in *Cynocephalus* [1] the digastricus anterior usually inserts onto the angle of the mandible. [-] Inapplicable in *Pongo*, because the digastricus anterior is usually not present as a distinct muscle.
6. *Tensor tympani* is not a distinct muscle (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Tupaia* [1] the tensor tympani is usually not present as a distinct muscle. *Colobus*, *Cercopithecus* and *Pongo* are coded as "?".
7. *Chorda tympani* passes above the *tensor tympani*. In *Rattus*, *Cynocephalus*, *Lemur*, *Propithecus*, *Loris* and *Tarsius* [0], the chorda tympani passes mainly below the tensor tympani (hypotensoric). In *Aotus*, *Callithrix*, *Saimiri*, *Pithecia*, *Macaca*, *Papio*, *Hylobates*, *Gorilla*, *Pan* and *Homo* [1], it passes mainly above the muscle (epitensoric). *Nycticebus*, *Colobus*, *Cercopithecus* and *Pongo* are coded as "?". [-] Inapplicable in *Tupaia*, because the tensor tympani is usually not present as a distinct muscle.
8. *Temporalis* has a *pars suprazygomatica*. Contrary to taxa of CS-0 [0], in *Tupaia*, *Lemur*, *Propithecus*, *Loris*, *Nycticebus*, *Tarsius*, *Aotus*, *Callithrix*, *Saimiri*, *Pithecia*, *Colobus*, *Cercopithecus*, and *Papio* [1] there is a distinct *pars suprazygomatica* of the temporalis. *Macaca* and *Gorilla* are coded here as "?".
9. *Pterygoideus lateralis* has well differentiated inferior and superior heads. Contrary taxa of CS-0 [0], in *Aotus*, *Pithecia*, *Saimiri*, *Macaca*, *Papio*, *Colobus*, *Cercopithecus*, *Hylobates*, *Pongo*, *Gorilla*, *Pan* and *Homo* [1] the pterygoideus lateralis is usually well differentiated into distinct superior and inferior heads. *Loris* and *Nycticebus* are coded as "?".

Hyoid muscles

10. *Stylohyoideus* is not a distinct muscle. Contrary to taxa of CS-0 [0], in *Cynocephalus*, *Saimiri* and *Callithrix* [1] the stylohyoideus is usually not present as a distinct muscle.
11. *Stylohyoideus* is partially pierced by the *digastricus posterior* and/or by the intermediate digastric tendon. Contrary to taxa of CS-0 [0], in *Tupaia*, *Cercopithecus*, *Papio*, *Colobus*, *Gorilla*, *Pan* and *Homo* [1] the stylohyoideus is usually partially pierced by the digastricus posterior and/or by the intermediate digastric tendon. *Macaca* and *Pithecia* are coded as "?". [-] Inapplicable in *Cynocephalus*, *Saimiri* and *Callithrix* because the stylohyoideus is usually not present as a distinct muscle.
12. *Stylohyoideus* is inserted near the midline. Contrary to taxa of CS-0 [0], in *Propithecus* and *Lemur* [1] the distal insertion of the stylohyoideus onto the hyoid bone is peculiarly situated near the midline (i.e., the muscle almost reaches, or sometimes even contacts, its counterpart medially). [-] Inapplicable in *Cynocephalus*, *Saimiri* and *Callithrix* because the stylohyoideus is usually not present as a distinct muscle.

13. *Stylolaryngeus* is a distinct muscle (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], orangutans [1] usually have a distinct stylolaryngeus muscle that runs from the styloid process to the laryngeal sac.
14. *Digastricus posterior* is directly attached onto the mandible (AUTAPOMORPHY). Contrary to taxa of CS-0 (in which the anterior portion of the digastricus posterior is usually connected to the posterior portion of the digastricus anterior) [0], in *Pongo* [1] the anterior portion of the digastricus posterior is usually directly attached onto the back of the mandible.
15. *Jugulohyoideus* is not a distinct muscle. Contrary to taxa of CS-0 [0], in *Rattus*, *Tarsius*, *Aotus*, *Callithrix*, *Pithecia*, *Saimiri*, *Macaca*, *Colobus*, *Papio*, *Cercopithecus* and hominoids [1], the jugulohyoideus (often designated as 'mastoideostyloideus', mainly running from the mastoid process and/or adjacent regions to the hyoid apparatus and/or the ligaments connecting this apparatus to the cranium) is usually not present as a distinct muscle. *Loris* is coded as "?".
16. *Platysma cervicale* is not a distinct muscle. Contrary to taxa of CS-0 [0], in *Pan*, *Homo* and *Gorilla* [1] the platysma cervicale is usually markedly reduced or completely missing.
17. *Platysma myoides* is divided into a superior, superficial bundle, and an inferior, deep bundle. Contrary to taxa of CS-0 [0], in *Macaca*, *Papio* and *Cercopithecus* [1] the platysma myoides is mainly divided into a superior, superficial bundle and an inferior, deeper bundle, which are essentially separated by a well-developed cheek pouch.
18. 'Cervico-auriculo-occipitalis' is not a distinct bundle of the *occipitalis*. Contrary to taxa of CS-0 [0], in *Homo*, *Pan*, *Pongo* and *Gorilla* [1] the occipitalis is usually not differentiated into a main body (or 'occipitalis proprius') and a 'cervico-auriculo-occipitalis' (which is a lateral/superficial bundle of the occipitalis that often runs anterolaterally from the occipital region to the posterior portion of the ear and that sometimes covers part of the auricularis posterior in lateral view).
19. *Auricularis posterior* is not a distinct muscle (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in orangutans [1] the auricularis posterior is usually not present as a distinct muscle.
20. *Mandibulo-auricularis* is not a distinct muscle. Contrary to taxa of CS-0 [0], in *Cynocephalus*, *Tarsius*, and the anthropoid primates included in this study [1] there is usually no distinct, fleshy muscle mandibulo-auricularis.
21. *Zygomatiko-auricularis* is a distinct muscle (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Tarsius* [1] the zygomatiko-auricularis is present as a distinct muscle.
22. *Risorius* is a distinct muscle. Contrary to taxa of CS-0 [0], in modern humans, *Gorilla* and *Pan* [1] the risorius is often present as a distinct muscle.
23. *Sphincter colli superficialis* is not a distinct muscle. Contrary to *Rattus* and *Tupaia* [0], in *Cynocephalus* and the primates included in this study [1] the sphincter colli superficialis is usually not present as a distinct muscle.
24. *Sphincter colli profundus* is not a distinct muscle. Contrary to taxa of CS-0 [0], in *Propithecus*, *Pithecia*, *Macaca*, *Papio*, *Colobus* and hominoids [1] the sphincter colli profundus is usually not present as a distinct muscle.
25. *Sternofacialis* is not a distinct muscle. Contrary to *Rattus* [0], in *Tupaia*, *Cynocephalus*, and the primates included in this study [1] the sternofacialis is usually not present as a distinct muscle.
26. *Interscutularis* is not a distinct muscle. Contrary to *Rattus* [0], in *Tupaia*, *Cynocephalus*, and the primates included in this study [1] the interscutularis is usually not present as a distinct muscle.
27. '*Zygomatikus*' is the only well developed zygomatic muscle in the cheek region. *Callithrix*, *Aotus*, *Saimiri* and *Pithecia* [1], usually have a derived condition that is not found in taxa of CS-0 [0]: they only have a well developed 'zygomatikus' muscle in the cheek region (and not two, i.e. a zygomatikus major and a zygomatikus minor).
28. Anterior portion of *zygomatikus major* passes partially or completely deep to the *levator anguli oris facialis*. In taxa of CS-0 the anterior portion (i.e., the portion attaching on the angle of the mouth) of the zygomatikus major or of the lower part of the 'zygomatikus' (in New World monkeys) is superficial to the levator anguli oris facialis [0]. In *Cercopithecus*, *Macaca*, *Papio* and *Hylobates* [1] it usually passes at least partially deep to this latter muscle.
29. *Zygomatikus major* is almost completely covered by the *platysma myoides* and/or the *platysma cervicale* (AUTAPOMORPHY). [0] In taxa of CS-0 the zygomatikus major (or the lower portion of the 'zygomatikus' in New World monkeys) and the platysma (myoides and/or cervicale) essentially lie at the same level or the former is partially/completely superficial to the latter, or, also often, the former lies mainly superiorly

- to the latter. In *Tupaia* [1] the zygomaticus major is usually almost completely covered by the platysma myoides and/or the platysma cervicale in lateral view. *Tarsius* is coded as "?".
30. **Zygomaticus minor** is directly originated from the ear. Contrary to taxa of CS-0 [0], in *Tupaia*, *Aotus*, *Callithrix*, *Propithecus*, *Lemur*, *Nycticebus*, *Loris* and *Tarsius* [1] the zygomaticus minor (or the upper portion of the 'zygomaticus', in New World monkeys) is directly originated from the ear.
 31. **Zygomaticus major** is not directly originated from the ear. Contrary to taxa of CS-0 [0], in *Saimiri*, *Pithecia*, *Cercopithecus*, *Macaca*, *Colobus*, *Papio* and hominoids [1], the zygomaticus major (or the lower portion of the zygomaticus in New World monkeys) is not directly originated from the ear. [-] Inapplicable in *Aotus* and *Callithrix*, because their muscle zygomaticus does reach the ear but these two taxa were already coded for that feature in the character above (within all the anthropoids included in this cladistic analysis, they are the only two genera in which there is a direct attachment onto the ear, and coding them together again in the present character would thus mean to code them together twice, although this clearly refers to a single feature, i.e., having the zygomaticus muscle attached onto the ear).
 32. **Frontalis** is a distinct muscle. Contrary to *Rattus* and *Saimiri* [0], in *Tupaia*, *Cynocephalus* and the other primate taxa included in this study [1] the frontalis is usually present as a distinct muscle.
 33. **Auricularis superior** is a distinct muscle. Contrary to *Rattus* [0], in *Tupaia*, *Cynocephalus* and the primates included in this study [1] the auricularis superior is usually present as a distinct muscle.
 34. **Zygomatoco-orbicularis** is a distinct muscle. Contrary to taxa of CS-0 [0], in *Tupaia* and *Cynocephalus* [1] the zygomatoco-orbicularis is usually present as a distinct muscle.
 35. **Depressor supercillii** is a distinct muscle. Contrary to *Rattus*, *Tupaia* and *Cynocephalus* [0], in the primate taxa included in this study [1] the depressor supercillii is usually present as a distinct muscle.
 36. **Corrugator supercillii** is a distinct muscle. Contrary to *Rattus* [0], in *Tupaia*, *Cynocephalus* and all primate taxa included in this cladistic analysis (except *Saimiri*, which is coded as "?") [1] the corrugator supercillii is usually present as a distinct muscle.
 37. **Levator labii superioris** runs mainly superoinferiorly from the region below the eye to the upper lip. [0] In the non-catarrhine taxa included in this analysis, but also in *Hylobates*, the levator labii superioris is not as markedly vertical (superoinferiorly directed) as is the case in taxa of CS-1: it mainly runs, instead, posteroanteriorly and lateromedially from the infraorbital region to the nose. [1] In the non-hylobatid catarrhine taxa included in this study the levator labii superioris runs mainly superoinferiorly from the infraorbital region to the upper lip, being less connected to the nose.
 38. **Depressor septi nasi** is a distinct muscle. Contrary to taxa of CS-0 [0], in the catarrhines included in this study [1] the depressor septi nasi is usually present as a distinct muscle.
 39. **Depressor anguli oris** is a distinct muscle. Contrary to taxa of CS-0 [0], in *Aotus* and the catarrhines included in this study [1] the depressor anguli oris is usually present as a distinct muscle.
 40. **Mentalis** is not a distinct muscle (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Rattus* [1] the mentalis is usually not present as a distinct muscle.

Branchial muscles

41. **Stylopharyngeus** originates from the stylomandibular ligament. In taxa of CS-0 [0] the stylopharyngeus usually originates from the cranium and from ligamentous, cartilaginous or ossified structures of the hyoid apparatus such as the stylohyal ligament. In *Callithrix* and *Saimiri* [1] a substantial part of the stylopharyngeus is originated from the stylomandibular ligament instead. *Pithecia* is coded as "?".
42. **Ceratohyoideus** is not a distinct muscle. Contrary to taxa of CS-0 [0], in hominoids and *Colobus* [1] the ceratohyoideus is usually not present as a distinct muscle. *Loris*, *Nycticebus* and *Papio* are coded as "?".
43. **Spinotrapezius** is not a distinct muscle. Contrary to *Rattus* and *Tarsius* [0], in *Cynocephalus*, *Tupaia*, and the non-tarsoid primates included in this study [1] the spinotrapezius is not present as a distinct muscle (i.e., there is a single, continuous muscle trapezius).
44. **Cleido-occipitalis** is not a distinct muscle. Contrary to *Rattus* and *Tarsius* [0], in *Cynocephalus* and the primates included in this study [1] the cleido-occipitalis is usually not present as a distinct muscle.
45. **Trapezius** inserts onto the clavicle. Contrary to taxa of CS-0 [0], in *Loris*, *Nycticebus*, *Pithecia*, *Saimiri*, *Aotus*, *Macaca*, *Colobus*, *Papio*, *Cercopithecus*, and hominoids [1] the trapezius usually attaches onto the clavicle. *Propithecus* is coded as "?".
46. **Trapezius** inserts onto \geq lateral 1/3 of the clavicle. [0] Within those primates included in this study with an insertion of the trapezius onto the clavicle, an insertion onto less than the lateral 1/3 of the clavicle is usually found in *Macaca*, *Pithecia*, *Saimiri*, *Aotus*, *Colobus* and *Cercopithecus*. [1] In *Nycticebus*, *Loris*,

- Papio* and hominoids the muscle goes to the lateral 1/3, or to more than the lateral 1/3, of the clavicle. *Propithecus* is coded as "?". [-] Inapplicable in taxa in which there is no insertion onto the clavicle (see character above).
47. **Trapezius** does not insert onto the acromion (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Tupaia* [1] the trapezius usually does not insert onto the acromion. *Tarsius* is coded as "?".
 48. **Trapezius** does not originate from the cranium. Contrary to taxa of CS-0 [0], in *Rattus*, *Cynocephalus*, *Lemur*, *Propithecus*, *Tarsius*, *Callithrix*, and *Hylobates* [1] the trapezius is usually not directly originated from the cranium.
 49. **Sternocleidomastoideus** is hypertrophied (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Tarsius* [1] the sternocleidomastoideus is hypertrophied and has a peculiar, wide contact with its counterpart in the dorsal midline (of the nuchal/occipital region).
 50. **Constrictor pharyngis medius** has no pars ceratopharyngea (AUTAPOMORPHY). [0] In *Tupaia*, *Cynocephalus*, *Lemur*, *Propithecus*, *Tarsius*, *Aotus*, *Callithrix*, *Pithecia*, *Saimiri*, *Macaca*, *Papio*, *Cercopithecus*, *Colobus*, *Hylobates*, *Gorilla*, *Homo* and *Pan*, the constrictor pharyngis medius is at least partially attached onto the greater horn of the hyoid bone, i.e. it has a pars ceratopharyngea. [1] In *Rattus* the constrictor pharyngis medius is not partially attached to the greater horn of the hyoid bone. *Pongo*, *Loris* and *Nycticebus* are coded as "?".
 51. **Cricothyroideus** is differentiated into a pars recta and a pars obliqua. Contrary to taxa of CS-0 [0], in the primate taxa included in this study (except *Nycticebus*, which is coded as "?") [1] the cricothyroideus usually has a distinct pars obliqua and a distinct pars recta.
 52. **Thyroideus transversus** is a distinct muscle (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Hylobates* [1] there is often a distinct muscle thyroideus transversus (also designated in the literature as 'thyroideus impar'), which lies on the ventral margin, and runs transversely to connect the posteroventromedial portion of the two sides, of the larynx.
 53. **Pterygopharyngeus** is not a distinct muscle. Contrary to *Rattus*, *Cynocephalus* and *Hylobates* [0], in *Tupaia*, *Lemur*, *Propithecus*, *Tarsius* and the non-hylobatid anthropoids included in this study [1] the pterygopharyngeus is either missing or fused with the constrictor pharyngis superior. *Loris* and *Nycticebus* are coded as "?".
 54. **Thyroarytenoideus** is not differentiated into a pars superior and a pars inferior. [0] In taxa of CS-0 the thyroarytenoideus is mainly divided into a more superior, and often lateral, pars superior - often also named 'pars lateralis' or 'pars externa' or 'ventricularis' -, and a more inferior, and often mesial, pars inferior - often also named 'pars medialis' or 'pars interna' or 'vocalis'. [1] In *Callithrix*, *Aotus*, *Saimiri*, *Macaca*, *Papio*, *Cercopithecus*, *Colobus* and non-hylobatid hominoids the pars superior and pars inferior are not present as distinct structures. *Loris*, *Nycticebus*, *Pithecia* and *Hylobates* are coded as "?".
 55. **Arytenoideus obliquus** is a distinct muscle. Contrary to taxa of CS-0 [0], in *Pongo*, *Gorilla*, *Pan* and *Homo* [1] the arytenoideus obliquus is often present as a distinct muscle.
 56. **Cricoarytenoideus posterior** does not meet its counterpart at the dorsal midline. Contrary to taxa of CS-0 [0], in *Homo*, *Pan*, *Gorilla*, *Papio*, *Colobus*, *Cercopithecus*, *Callithrix*, *Pithecia*, *Aotus* and *Saimiri* [1] the cricoarytenoideus posterior usually does not meet its counterpart at the dorsal midline. *Loris* and *Nycticebus* are coded as "?".

Hypobranchial muscles

57. **Geniohyoideus** is fused to its counterpart in the midline. [0] In taxa of CS-0 the geniohyoideus usually lies very close to its counterpart at the ventral midline, but it is separated from it by fascia, a median raphe, and/or some other type of tissue, so that the muscles of two sides are not fused. [1] Such a fusion is usually found in *Tupaia*, *Lemur*, *Propithecus*, *Nycticebus*, *Papio*, *Colobus*, *Cercopithecus*, *Homo* and *Pan*. *Loris* is coded as "?".
58. **Chondroglossus** is present as a distinct bundle of the **hyoglossus**. Contrary to taxa of CS-0 [0], in *Tupaia*, *Lemur*, *Propithecus*, *Pithecia*, *Macaca*, *Colobus*, *Cercopithecus*, and hominoids [1] the chondroglossus is usually present as a distinct bundle of the hyoglossus. *Papio*, *Nycticebus*, *Cynocephalus* and *Loris* are coded as "?".
59. **Hyoglossus** is partially or completely fused with the **thyrohyoideus**. Contrary to taxa of CS-0 [0], in *Cynocephalus*, *Aotus*, *Macaca* and *Papio* [1] the hyoglossus and thyrohyoideus are usually fused (partially or completely) to each other.

60. **Styloglossus** originates from the stylomandibular ligament (ordered multistate character). In taxa of CS-0 [0] the styloglossus usually originates from the cranium and from ligamentous, cartilaginous or ossified structures of the hyoid apparatus such as the stylohyal ligament. In *Aotus*, *Callithrix*, *Pithecia* and *Saimiri* the styloglossus is at least partially originated from the stylomandibular ligament, the origin from this ligament being however less substantial in *Aotus* and *Pithecia* [1] than in *Callithrix* and *Saimiri* [2]. *Papio* and *Cercopithecus* are coded as "?".
61. **Styloglossus** has a distinct oblique slip running anteroinferiorly to blend with the lateral portion of the **hyoglossus**. Contrary to taxa of CS-0 [0], in *Pan* and *Homo* [1] the styloglossus runs mainly longitudinally to insert onto the tongue but has a distinct oblique slip that runs anteroinferiorly at about 45° from the main body of the muscle to insert more inferiorly onto the lateral surface of the hyoglossus. *Pongo* is coded as "?".
62. **Sternohyoideus** is divided into two bundles (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Cynocephalus* [1] the sternohyoideus has a configuration in which there is a belly that is mainly inserted onto the thyroid cartilage and that then gives rise to another belly that reaches the hyoid bone.
63. **Sternohyoideus** does not contact nor lie against its counterpart for most of its length. Contrary to taxa of CS-0 [0], in *Cynocephalus*, *Pan* and *Homo* [1] the sternohyoideus usually does not contact, nor lies just next to, its counterpart for most of its length. *Hylobates*, *Nycticebus* and *Loris* are coded as "?".
64. Anterior portion of **sternothyroideus** extends anteriorly to the posterior portion of the **thyrohyoideus**. Contrary to taxa of CS-0 [0], in *Rattus*, *Callithrix*, *Hylobates*, *Gorilla*, and *Pan* [1] the main body of the sternothyroideus is usually extended anteriorly, so that its anterior portion is anterior to the posterior portion of the main body of the thyrohyoideus. *Pongo*, *Nycticebus* and *Loris* are coded as "?".
65. **Omohyoideus** is not a distinct muscle. Contrary to taxa of CS-0 [0], in *Cynocephalus*, *Colobus* and *Cercopithecus* [1] the omohyoideus is usually not present as a distinct muscle. *Aotus* is coded as "?".
66. **Omohyoideus** has an intermediate tendon. Contrary to taxa of CS-0 [0], in *Tupaia*, *Pan* and *Homo* [1] the intermediate tendon of the omohyoideus is usually present. *Aotus* is coded as "?". [-] Inapplicable in *Cynocephalus*, *Colobus* and *Cercopithecus*, because the omohyoideus is usually not present as a distinct muscle.
67. **Omohyoideus** occasionally has three bellies. Contrary to taxa of CS-0 [0], in at least some specimens of *Gorilla*, *Pan* and *Homo* [1] the omohyoideus has three bellies (usually a superior belly, an inferomedial belly, and an inferolateral belly). *Aotus* is coded as "?". [-] Inapplicable in *Cynocephalus*, *Colobus* and *Cercopithecus*, because the omohyoideus is usually not present as a distinct muscle.

Pectoral muscles

68. **Serratus anterior** and **levator scapulae** are separated (ordered multistate character). [0] In *Rattus*, *Cynocephalus*, *Tupaia*, *Nycticebus*, *Propithecus*, *Lemur* and *Loris*, the serratus anterior and levator scapulae are deeply blended. In *Tarsius*, *Aotus*, *Callithrix*, *Pithecia*, *Saimiri*, *Macaca*, *Papio*, *Cercopithecus* and *Colobus* [1] the two muscles are less blended distally (at their insertion onto the scapula) than in taxa of CS-0, but more blended proximally than in hominoids [2], in which the two muscles are well separated.
69. **Rhomboideus major** and **rhomboideus minor** are not distinct muscles. Contrary to taxa of CS-0 [0], in *Cynocephalus*, *Lemur*, *Propithecus*, *Loris*, *Nycticebus*, *Tarsius*, *Aotus*, *Pithecia*, *Saimiri* and non-human hominoids [1] the rhomboideus major and rhomboideus minor are not present as distinct muscles (i.e. these taxa have, instead, a single, undivided muscle rhomboideus). *Colobus* is coded as "?".
70. **Rhomboideus occipitalis** is not a distinct muscle. Contrary to taxa of CS-0 [0], in *Cynocephalus*, *Hylobates*, *Gorilla*, *Pan* and *Homo* [1] the rhomboideus occipitalis is usually not present as a distinct muscle. *Propithecus* is coded as "?".
71. **Levator scapulae** does not extend to C5. Contrary to taxa of CS-0 [0], in hominoids [1] the origin of the levator scapulae usually does not extend posteriorly to C5. *Nycticebus* is coded as "?".
72. **Levator claviculae** is not a distinct muscle (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in modern humans [1] the levator claviculae is usually not present as distinct muscle.
73. **Atlantoscapularis posticus** is a distinct muscle (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], *Tupaia* [1] has a muscle atlantoscapularis posticus. [-] This character is inapplicable in modern humans because the levator claviculae is usually not present as a distinct muscle.

74. **Levator claviculae** inserts onto the clavicle. Contrary to taxa of CS-0 [0], in *Colobus* and non-human hominoids [1] the levator claviculae is at least partially attached onto the clavicle. [-] This character is inapplicable in modern humans, because the levator claviculae is usually not present as a distinct muscle.
75. **Levator claviculae** inserts deep to the insertion of the **trapezius**. Contrary to taxa of CS-0 [0], in *Saimiri*, *Pithecia*, and the non-human catarrhines included in this study [1] the levator claviculae is usually deep to (covered either laterally or dorsally by) the trapezius. [-] This character is inapplicable in modern humans, because the levator claviculae is usually not present as a distinct muscle.
76. **Levator claviculae** inserts onto a more medial portion of the clavicle (uninformative). In *Hylobates* [0] the insertion of the levator claviculae on the clavicle is considerably more lateral than in other non-human hominoids and in *Colobus* [1] (e.g., previous studies have reported a position index, from acromial end of clavicle, of 18.3 in *Hylobates*, contrary to, 38.2 and 38.4 in *Gorilla* and *Pan*, respectively; also corroborated by our dissections of specimens of these three taxa and of the other terminal taxa included in this study). [-] This character is inapplicable in taxa where the levator claviculae is not present as a distinct muscle or where this muscle is present but does not insert onto the clavicle (see characters above).
77. **Subclavius** originates from the third rib (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Hylobates* [1] the origin of the subclavius often extends to rib 3 and/or its costal cartilage.
78. **Pectoralis major** has no clavicular origin. Contrary to taxa of CS-0 [0], in *Loris*, *Nycticebus*, *Aotus*, *Callithrix*, *Saimiri*, *Macaca*, *Cercopithecus* and *Pongo* [1] there is usually no clavicular origin of the pectoralis major. *Papio* and *Pithecia* are coded as "?".
79. '**Pectoralis tertius**' a distinct muscle (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Rattus* [1] there is a distinct 'pectoralis tertius', which usually runs from the xiphoid process to the coracoid process of the scapula.
80. **Pectoralis major** inserts onto the coracoid process (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Gorilla* [1] the abdominal head of the pectoralis major is usually at least partially inserted onto the coracoid process.
81. **Pectoralis major** is blended with the **biceps brachii**. Contrary to taxa of CS-0 [0], in *Gorilla* and *Hylobates* [1] the abdominal head of the pectoralis major is usually blended with the biceps brachii.
82. **Pectoralis major** has a pars capsularis in at least some specimens. Contrary to taxa of CS-0 [0], in *Aotus*, *Saimiri* and *Pithecia* [1] there is a distinct pars capsularis of the pectoralis major, which lies laterally to the main body of the muscle and is often separated from this main body by the cephalic vein. *Callithrix* is coded as "?".
83. **Pectoralis minor** inserts onto the coracoid process. Contrary to taxa of CS-0 [0], in *Rattus*, *Cynocephalus*, *Aotus*, *Saimiri*, *Hylobates*, *Pongo*, *Gorilla* and modern humans [1] the pectoralis minor is at least partially inserted onto the coracoid process. *Papio* and *Macaca* are coded as "?".
84. **Pectoralis minor** inserts onto the clavicle (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Hylobates* [1] the pectoralis minor is often at least partially inserted onto the clavicle.
85. **Panniculus carnosus** is not a distinct muscle. Contrary to taxa of CS-0 [0], *Pithecia* and hominoids [1] normally do not have a panniculus carnosus.
86. **Deltoideus** is a single, continuous muscle. [0] In taxa of CS-0 the deltoideus complex is usually divided into a deltoideus scapularis and a deltoideus acromialis et clavicularis, which can be further differentiated into two distinct muscles, the deltoideus acromialis and the deltoideus acromialis. [1] In the anthropoid primates included in this study, as well as in *Propithecus*, *Loris* and *Nycticebus* there is a single, continuous deltoideus muscle.
87. **Teres minor** is not a distinct muscle (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Tupaia* [1] the teres minor is almost always absent as a distinct structure (being probably fused with the infraspinatus and/or the deltoideus scapularis).
88. **Subscapularis** has a distinct pars posterioris (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], *Hylobates* [1] has a distinct, peculiar pars inferioris of the subscapularis, which is partially separated, medially, from the main, anterior portion of the muscle by a ridge of the scapula.
89. **Latissimus dorsi** and **teres major** are fused. [0] In taxa of CS-0 the distal tendon of the latissimus dorsi passes mainly dorsal to (and is not fused with) the distal tendon of the latissimus dorsi. [1] In *Tupaia*, *Pongo*, *Hylobates* and the Old World monkey genera included in this study [1] the distal tendons of the latissimus dorsi and of the teres major are usually partially or completely fused to each other, at their insertions onto the humerus.

Arm muscles

90. **Dorsoepitrochlearis** has two distinct proximal heads originating from the *latissimus dorsi* and the *teres major* (AUTAPOMORPHY). Contrary to taxa of CS-O [0], *Tupaia* [1] has a peculiar configuration in which the dorsoepitrochlearis has two distinct proximal heads, one originating from the *teres major* and the other from the *latissimus dorsi*. [-] This character is inapplicable in modern humans because the dorsoepitrochlearis is usually not present as a distinct muscle (see character below).
91. **Dorsoepitrochlearis** is not a distinct muscle (AUTAPOMORPHY). Contrary to taxa of CS-O [0], in modern humans [1] the dorsoepitrochlearis is usually not present as a distinct muscle.
92. **Dorsoepitrochlearis** does not insert onto the olecranon process of the ulna. Contrary to taxa of CS-O [0], in non-human hominoids [1] the dorsoepitrochlearis is usually mainly attached onto the medial epicondyle, the intermuscular septum and/or other surrounding structures, but not onto the olecranon process or the olecranon fascia. [-] This character is inapplicable in modern humans because the dorsoepitrochlearis is usually not present as a distinct muscle.
93. **Dorsoepitrochlearis** is blended with the **biceps brachii** (AUTAPOMORPHY). Contrary to taxa of CS-O [0], in *Hylobates* [1] the dorsoepitrochlearis is usually deeply blended with the short head of the biceps brachii.
94. Strong fascial connection between the **dorsoepitrochlearis** and the subscapular fascia and/or the scapula is present. Contrary to taxa of CS-O [0], in *Aotus*, *Callithrix*, *Pithecia* and *Saimiri* [1] there is usually a strong fascial connection between the dorsoepitrochlearis and the subscapular fascia and/or scapula.
95. Long head of **triceps brachii** is divided into a thinner, deep bundle and a broader, superficial bundle (AUTAPOMORPHY). Contrary to taxa of CS-O [0], in *Papio* [1] the long head of the triceps brachii is often peculiarly differentiated into a thinner, deep (ventral) bundle and a broader, superficial (dorsal) bundle.
96. **Triceps brachii** has a posterior head. [0] In taxa of CS-O the triceps brachii is usually only differentiated into three main divisions (i.e. a long head, a lateral head, and a medial head, although some of this divisions may sometimes be partially differentiated into subdivisions). [1] In *Tupaia*, *Lemur*, *Propithecus*, *Loris*, *Nycticebus* and *Tarsius* the triceps brachii has a lateral head, a medial head, a long head, and also a distinct, peculiar posterior head.
97. Long head of **triceps brachii** originates from half or more than half of the lateral border of the scapula. Contrary to taxa of CS-O [0], in *Macaca*, *Colobus*, *Cercopithecus*, *Papio*, *Pongo*, and *Pan* [1] the long head of the triceps brachii usually originates from half or more than half of the lateral border of the scapula. *Gorilla* is coded as "?".
98. Strong fascial connection between the **triceps brachii** and the scapular spine and/or the axillary region is present. Contrary to taxa of CS-O [0], in *Lemur*, *Loris*, *Nycticebus*, *Aotus*, *Callithrix*, *Saimiri* and *Pithecia* [1] there is usually a peculiar, strong fascial connection between the triceps brachii and the scapular spine and/or axillary region.
99. **Brachialis** does not originate from the surgical neck of the humerus. Contrary to taxa of CS-O [0], in *Cynocephalus*, *Loris*, *Nycticebus*, *Callithrix*, *Pithecia*, *Saimiri*, *Aotus*, *Papio*, *Colobus*, *Cercopithecus* and hominoids [1] the origin of the brachialis usually does not extend (i.e., it is distal) to the surgical neck of the humerus. *Macaca* is coded as "?".
100. **Biceps brachii** has no short head. Contrary to taxa of CS-O (in which both short and long heads of biceps brachii are present) [0], in *Loris* and *Nycticebus* [1] the short head is usually missing.
101. Short and long heads of **biceps brachii** are completely separated (AUTAPOMORPHY). [0] Short and long heads of biceps brachii at least partially blended distally. [1] In *Tarsius* these two heads are often entirely separated. [-] Inapplicable in *Loris* and *Nycticebus*, because the short head of the biceps is usually missing.
102. Short head of **biceps brachii** originates from the humerus (AUTAPOMORPHY). [0] The short head of biceps brachii usually originates from the scapula. [1] In *Hylobates* the short head of the biceps brachii is usually at least partially originated from the humerus. [-] Inapplicable in *Loris* and *Nycticebus*, because the short head of the biceps is usually missing.
103. **Biceps brachii** is blended with the **flexor digitorum superficialis** (AUTAPOMORPHY). Contrary to taxa of CS-O [0], in *Hylobates* [1] the distal portion of the biceps brachii is deeply blended with the proximal portion of the flexor digitorum superficialis.

104. ***Biceps brachii*** does not insert onto the ulna. [0] In *Cynocephalus* and *Tupaia* the biceps brachii usually inserts directly onto both the ulna and the radius. [1] *Rattus* and the primate taxa included in this study the biceps brachii usually inserts directly onto the radius, but not onto the ulna.
105. ***Biceps brachii*** has no bicipital aponeurosis. [0] In taxa of CS-0 the biceps brachii is usually prolonged distally by a bicipital aponeurosis ('lacertus fibrosus' or 'lacertus carnosus'), which is commonly associated with the fascia covering forearm muscles such as the pronator teres. [1] In *Cynocephalus*, *Tupaia*, *Loris*, *Nycticebus*, *Tarsius*, *Callithrix*, *Saimiri*, *Pithecia*, *Papio*, *Colobus*, *Cercopithecus* and *Pongo* the bicipital aponeurosis is usually not present as a distinct structure. *Macaca* and *Aotus* are coded as "?".
106. Bicipital aponeurosis (of ***biceps brachii***) forms a 'lacertus carnosus' (AUTAPOMORPHY). [0] Within those taxa with a bicipital aponeurosis, this structure usually forms a 'lacertus fibrosus' (i.e., it does not include fleshy muscular fibers). [1] In *Hylobates* the bicipital aponeurosis is usually at least partially fleshy, thus forming a 'lacertus carnosus' between the main body of the biceps and the flexor muscles of the forearm. *Macaca* and *Aotus* are coded as "?". [-] This character is inapplicable in taxa that do not have a distinct bicipital aponeurosis (see character above).
107. ***Coracobrachialis profundus*** is not present as a distinct head of the ***coracobrachialis***. [0] In taxa of CS-0 the coracobrachialis proprius (or 'medius') and coracobrachialis profundus (or 'brevis') are present as distinct structures, the coracobrachialis profundus being usually a short bundle running from the coracoid process to the proximal region of the humerus and often lying deep (dorsal) to the coracobrachialis proprius. [1] In hominoids and in *Rattus* and *Pithecia* the coracobrachialis profundus is usually absent as a distinct structure.

Ventral (volar) forearm muscles

108. ***Pronator quadratus*** is not a distinct muscle (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Cynocephalus* [1] there is no distinct pronator quadratus.
109. ***Flexor pollicis longus*** is a distinct muscle. Contrary to taxa of CS-0 [0], in *Hylobates* and modern humans [1] the flexor pollicis longus is usually present as a distinct muscle (i.e., with an independent fleshy muscle that sends a tendon to digit 1 only).
110. ***Flexor digitorum profundus*** is not originated from the medial epicondyle of the humerus or from the common flexor tendon. [0] In taxa of CS-0 the flexor digitorum profundus (and/or the flexor pollicis longus in *Hylobates*) usually originates from the medial epicondyle of the humerus and/or from the common flexor tendon associated with this epicondyle, as well as from the radius, ulna and/or interosseous membrane. [1] In *Macaca*, *Pongo*, *Gorilla*, *Pan* and modern humans the origin of the flexor digitorum profundus (and of the flexor pollicis longus, in modern humans) is usually exclusively from the radius and/or ulna and, often, from the interosseous membrane. *Papio* and *Colobus* are coded as "?".
111. ***Flexor digitorum profundus*** is not innervated by the ulnar nerve. [0] In taxa of CS-0 the flexor digitorum profundus is usually at least partially innervated by the ulnar nerve. [1] In *Macaca*, *Papio* and *Colobus* the muscle is usually not innervated by the ulnar nerve. *Aotus*, *Callithrix*, *Saimiri* and *Cercopithecus* are coded as "?".
112. Tendon of ***flexor digitorum profundus*** to digit 1 is vestigial or absent. [0] In taxa of CS-0 the tendon of the flexor digitorum profundus to digit 1 (or the tendon of the flexor pollicis longus in *Hylobates* and *Homo*), is basically similar to the tendons of the flexor digitorum profundus to the other digits. [1] In *Colobus*, *Pongo*, *Gorilla* and *Pan* the tendon to digit 1 is vestigial (i.e. it is markedly shorter and/or thinner than that of taxa of CS-0) or absent.
113. ***Flexor digitorum superficialis*** originates from the radius. Contrary to taxa of CS-0 [0], in hominoids [1] the flexor digitorum superficialis usually partially originates from the radius.
114. ***Flexor digitorum superficialis*** originates from the ulna. Contrary to taxa of CS-0 [0], in hominoids [1] the flexor digitorum superficialis usually partially originates from the ulna.
115. ***Flexor digitorum superficialis*** inserts onto digit 5. [0] In *Rattus* and *Tupaia* the flexor digitorum superficialis usually inserts onto digits 2-4. [1]. In *Cynocephalus* and the primates included in this study this muscle is usually partially inserted onto digit 5.
116. ***Flexor digitorum superficialis*** does not insert onto digit 2 (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Loris* [1] the flexor digitorum superficialis usually does not insert onto digit 2.
117. ***Palmaris longus*** is hypertrophied (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Cynocephalus* [1] the palmaris longus is hypertrophied.

118. *Palmaris longus* is absent in > 5% of the cases. The palmaris longus is always, or almost always, present in the specimens of taxa of CS-0 [0], but it is absent in more than 5% of the cases in specimens of *Gorilla*, *Pan* and *Homo* [1].
119. *Flexor carpi ulnaris* does not originate from the humerus. [0] In taxa of CS-0 the flexor carpi ulnaris usually originates from the humerus (often from the medial epicondyle) and ulna (often from the coronoid process). [1] In *Cynocephalus* the muscle usually does not originate from the humerus. *Hylobates* is coded as "?".
120. *Epitrochleoanconeus* is not a distinct muscle. Contrary to taxa of CS-0 [0], in *Loris*, *Nycticebus*, *Hylobates*, *Pongo*, *Gorilla* and modern humans [1] the epitrochleoanconeus is usually not present as a separate, well-defined muscle. *Rattus* is coded as "?".
121. *Flexor carpi radialis* inserts onto the metacarpals II and III. [0] In taxa of CS-0 the flexor carpi radialis usually inserts onto metacarpal III (as is usually the case in, e.g., *Rattus*) or metacarpal II (as is usually the case in, e.g., *Lemur* and *Propithecus*) or, in a few cases, onto other structures (as is usually the case in, e.g., *Cynocephalus*), but usually does not attach onto both the metacarpal II and III. [1] In *Tupaia*, *Tarsius*, *Pithecia*, *Aotus*, *Callithrix*, *Saimiri*, *Macaca*, *Papio*, *Cercopithecus*, *Colobus*, *Pongo*, *Gorilla*, *Pan* and modern humans the muscle often inserts onto both metacarpals II and III. *Hylobates* is coded as "?".
122. *Flexor carpi radialis* does not insert onto the metacarpal II or the metacarpal III (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Cynocephalus* [1] the flexor carpi radialis does not attach to either metacarpal II or metacarpal III, being instead usually exclusively attached onto the trapezium and/or the trapezoid. *Loris* is coded as "?".
123. *Flexor carpi radialis* originates from the radius. [0] In taxa of CS-0 the flexor carpi radialis usually has a bony origin from the humerus, but not from the radius. [1] In *Pongo*, *Gorilla* and *Pan* the muscle has bony origins from at least the humerus and the radius. *Hylobates* is coded as "?".
124. *Pronator teres* originates from the ulna (ordered multistate character). [0] In taxa of CS-0 the pronator teres usually has a bony origin from the humerus, and not from the ulna. Within hominoids a bony origin from the ulna (in addition to an origin from the humerus) is "frequent" (i.e. often but not usually, that is, present in < 50% of the cases) in *Hylobates* [1] and the rule (i.e. usually, that is, present in \geq 50% of the cases) in *Pan*, *Gorilla*, *Pongo* and modern humans [2].

Hand muscles

125. *Palmaris brevis* is not a distinct muscle. Contrary to taxa of CS-0 [0], in *Hylobates* and *Pongo* [1] the palmaris brevis is usually not present as a distinct muscle.
126. *Palmaris brevis* is hypertrophied (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Colobus* [1] the palmaris brevis is hypertrophied, having two peculiar, distinct, well-developed heads, one on the ulnar side of the hand and the other on the radial side of the hand. [-] This character is inapplicable in *Hylobates* and *Pongo* because the palmaris brevis is usually absent (see character above).
127. *Flexor digitorum brevis manus* is a distinct muscle. Contrary to taxa of CS-0 [0], in *Cynocephalus* and *Tupaia* [1] the flexor digitorum brevis manus is usually present as a distinct structure.
128. *Lumbricales* originate from thin flexor digitorum profundus tendons (AUTAPOMORPHY). [0] In taxa of CS-0 the lumbricales are mainly originated directly from the main body of the insertion tendons of the flexor digitorum profundus. [1] In *Tarsius* these hand muscles are instead originated from peculiar, thin tendons that are, in turn, derived from the main body of the insertion tendons of the flexor digitorum profundus.
129. There are frequently three, or instead usually seven, lumbricales (unordered multistate character) (AUTAPOMORPHIES). [0] Taxa of CS-0 usually have four lumbricales, to digits 2-5. [1] In *Hylobates* the fourth lumbrical, i.e. the lumbrical going to digit 5, is frequently missing (i.e. it was missing in about 35% of the specimens dissected by others and by us). [2] *Cynocephalus* usually has a very unusual number of lumbricales, 7, which go to the radial and ulnar sides of digits 2, 3 and 4 and to the radial side of digit 5.
130. *Lumbricales* originate from the dorsal surfaces of the tendons of the flexor digitorum profundus (AUTAPOMORPHY). [0] In taxa of CS-0 the lumbricales are usually mainly originated from the ventral (palmar) surfaces of the tendons of the flexor digitorum profundus. [1] In *Hylobates* the lumbricales are mainly originated from the dorsal surfaces of these tendons.
131. *Contrahentes digitorum* are missing. Contrary to taxa of CS-0 [0], in *Pongo*, *Gorilla* and modern humans [1] there are usually no contrahentes digitorum other than the adductor pollicis.

132. *Two sets of **contrahentes digitorum** are present (AUTAPOMORPHY).* Contrary to taxa of CS-0 [0], *Tarsius* [1] usually has two sets of contrahentes. [-] Inapplicable in *Pongo*, *Gorilla* and modern humans because these in these taxa there are usually no contrahentes digitorum other than the adductor pollicis.
133. *There are more than two **contrahentes digitorum**.* [0] In taxa of CS-0 there are only two fleshy contrahentes (one to digit 2 and one to digit 5 in all these taxa except *Pan*, in which the contrahentes usually go to digits 4 and 5 instead). [1] In *Tarsius*, *Aotus*, *Callithrix*, *Pithecia*, *Saimiri*, *Macaca*, *Papio*, *Cercopithecus*, *Colobus* and *Hylobates*, there are three (to digits 2, 4 and 5 in all these taxa except *Tarsius*: see characters above) or eight (two sets, to digits 2, 3, 4 and 5, in *Tarsius*: see character and below). [-] Inapplicable in *Pongo*, *Gorilla* and modern humans because these in these taxa there are usually no contrahentes digitorum other than the adductor pollicis.
134. *There are **contrahentes digitorum** to digits 2, 3, 4 and 5 (AUTAPOMORPHY).* Contrary to taxa of CS-0 [0], *Tarsius* [1] has an unique condition in which there are contrahentes to digits 2-5 (see character above). [-] Inapplicable in *Pongo*, *Gorilla* and modern humans because these in these taxa there are usually no contrahentes digitorum other than the adductor pollicis.
135. ***Contrahentes digitorum** have a peculiar configuration (AUTAPOMORPHY).* Contrary to taxa of CS-0 [0], in *Tarsius* [1] the contrahentes have a peculiar configuration, arising from the palm and passing to the proximal and distal phalanges of all the five digits and, in addition, passing from some of the digits to the proximal phalanx of an adjacent digit. [-] Inapplicable in *Pongo*, *Gorilla* and modern humans because these in these taxa there are usually no contrahentes digitorum other than the adductor pollicis.
136. ***Thin, deep additional slip of adductor pollicis (TDAS-AD, or 'interosseous volaris primus of Henle' of modern human anatomy) is present (ordered multistate character).*** [0] TDAS-AD not described in the literature nor found in any dissections. [1] In *Gorilla* and *Pan* the TDAS-AD is present in some, but not in most, cases (i.e., in < 50% of the cases). [2] In modern humans the TDAS-AD is usually present (i.e. in \geq 50% of the cases).
137. ***Main body of adductor pollicis inserts onto much of metacarpal I (AUTAPOMORPHY).*** [0] In taxa of CS-0 the most proximal area of insertion of the main body of the adductor pollicis (i.e. excluding the TDAS-AD, when this structure is present) is usually onto the proximal phalanx of the thumb, the metacarpophalangeal joint and/or the sesamoid bones lying near to this joint and/or eventually onto a small portion of the distal margin of metacarpal I, as well as eventually onto the distal phalanx of the thumb. [1] In *Hylobates* the adductor pollicis is directly inserted onto much of metacarpal I (i.e. functionally the muscle becomes an 'adductor' but also an 'opponens' of the thumb).
138. ***Adductor pollicis has transverse and oblique heads (ordered multistate character).*** [0] In taxa of CS-0 the adductor pollicis is usually not differentiated into distinct transverse and oblique heads. In hominoids and the Old World monkeys *Papio*, *Colobus*, *Cercopithecus* and *Macaca* [2] the adductor pollicis had distinct oblique and transverse heads; in *Tarsius*, *Aotus*, *Saimiri* and *Pithecia* [1] the adductor pollicis is partly differentiated into oblique and transverse heads, particularly at its origin from metacarpal III and the contrahens fascia, but distally the two heads are blended (i.e. the differentiation is not as marked as in taxa scored as CS-2). *Callithrix* is coded as "?".
139. ***Flexor brevis profundus 2 is not a distinct muscle.*** Contrary to taxa of CS-0 [0], in *Tupaia*, *Cynocephalus*, *Aotus*, *Callithrix*, *Pithecia* and *Saimiri* [1] the flexor brevis profundus 2 is usually not present as a distinct structure (i.e., it is either missing or completely fused with the part of the flexor brevis profundus 1 that forms the main body of the undivided 'flexor pollicis brevis' of these taxa).
140. ***Flexores breves profundus are fused with the intermetacarpales, forming the dorsal interossei.*** Contrary to taxa of CS-0 [0], in *Tupaia*, *Cynocephalus*, *Aotus*, *Callithrix*, *Pithecia*, *Saimiri*, *Hylobates*, *Pongo*, *Gorilla* and modern humans [1] the flexores breves profundus 3, 5, 6 and 8 are usually fused with the intermetacarpales 1, 2, 3 and 4, forming the dorsal interossei 1, 2, 3 and 4, respectively.
141. ***Digit 4 is functional axis of intermetacarpales/dorsal interossei.*** [0] In taxa of CS-0 the intermetacarpales/dorsal interossei are inserted onto the radial sides of digits 2 and 3 and the ulnar sides of digits 3 and 4 (i.e. their functional axis is digit 3). [1] In *Lemur*, *Propithecus*, *Nycticebus* and *Loris* the insertion is usually onto the radial sides of digits 2, 3 and 4 and the ulnar side of digit 4 (i.e. the functional axis is digit 4).
142. ***Interossei accessorii are present.*** Contrary to taxa of CS-0 [0], *Nycticebus*, *Loris*, *Lemur*, *Propithecus* and *Hylobates* [1] usually have interossei accessorii. *Tarsius* is coded as "?".
143. ***Opponens pollicis is a distinct muscle.*** Contrary to taxa of CS-0 [0], in *Pithecia*, *Aotus*, *Saimiri*, *Tarsius* and the strepsirrhine and catarrhine primates included in this study [1] there is usually a distinct opponens pollicis.

144. ***Opponens pollicis*** reaches the distal portion of metacarpal I. [0] In *Lemur*, *Propithecus*, *Tarsius*, *Aotus*, *Pithecia* and *Saimiri* the opponens pollicis usually inserts onto metacarpal I but does not reach the distal portion of this bone. [1] In *Loris*, *Nycticebus*, *Macaca*, *Papio*, *Colobus*, *Cercopithecus* and hominoids the opponens pollicis usually extends to the distal portion of metacarpal I, inserting partially, or exclusively, onto this distal portion and/or onto the phalanges of the thumb. [-] Inapplicable in taxa in which the opponens pollicis is usually not present as a distinct muscle (see character above).
145. ***Opponens pollicis*** inserts onto the proximal and/or the distal phalanges of the thumb (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Hylobates* [1] the opponens pollicis is often partially inserted onto the proximal and/or distal phalanges of the thumb. [-] Inapplicable in taxa in which the opponens pollicis is not present as a distinct muscle or in which this muscle does not extend distally to the proximal portion of metacarpal I (see characters above).
146. ***Flexor digiti minimi brevis*** is partly originated from the pisiform. [0] In taxa of CS-0 the flexor digiti minimi brevis usually originates from the hamate, flexor retinaculum and/or surrounding structures such as the metacarpal V, but not from the pisiform. [1] In *Cynocephalus* and *Hylobates* the muscle is often partially originated from the pisiform.
147. ***Flexor digiti minimi brevis*** inserts onto the middle phalanx and/or the distal phalanx of digit 5. Contrary to taxa of CS-0, in which the flexor digiti minimi brevis inserts mainly onto the metacarpophalangeal joint, the base or middle of the proximal phalanx and/or the extensor expansion of digit 5 [0], in *Hylobates* and *Nycticebus* this muscle is often also inserted onto the middle phalanx and/or the distal phalanx of digit 5 [1]. *Loris* is coded as "?".
148. ***Opponens digiti minimi*** is a distinct muscle. Contrary to taxa of CS-0 [0], in *Rattus* and the primates included in this study [1] the opponens digiti minimi is present as a distinct muscle.
149. ***Opponens digiti minimi*** is divided into superficial and deep bundles (ordered multistate character). [0] Within those taxa with an opponens digiti minimi, in *Rattus* and the non-Catarrhini primates included in this study, the muscle is usually undivided. In hominoids [1] the muscle is usually slightly differentiated into superficial and deep bundles, while in *Papio*, *Colobus*, *Cercopithecus* and *Macaca* [2] the muscle is remarkably divided into a more superficial head and a deeper and broader head that, due to their peculiar differentiation, are often considered to be different muscles. [-] Inapplicable in *Tupaia* and *Cynocephalus*, in which the opponens digiti minimi is not present as a distinct muscle (see character above).
150. **Insertion of *opponens digiti minimi*** extends proximally to the distal part of metacarpal V. Contrary to *Rattus* [0], in the primates included in this study [1] the insertion of the opponens digiti minimi extends to the distal portion of metacarpal V, the muscle being thus inserted along most, or the whole, proximodistal length of this bone. [-] Inapplicable in *Cynocephalus* and *Tupaia*, in which the opponens digiti minimi is not present as a distinct muscle.
151. ***Abductor digiti minimi*** is divided into two well differentiated heads. Contrary to taxa of CS-0 [0], in *Macaca* and *Papio* [1] there is often a differentiation of the abductor digiti minimi into two heads, which in some cases are so markedly separated from each other that they are only connected through their distal tendons. *Homo* is coded as "?".

Dorsal forearm muscles

152. ***Brachioradialis*** often inserts onto the trapezium (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Tarsius* [1] the brachioradialis is often inserted onto the trapezium.
153. ***Extensor carpi radialis longus*** does not insert onto the metacarpal II (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Cynocephalus* [1] the extensor carpi radialis longus is not inserted onto the metacarpal II, being usually exclusively inserted onto the trapezium.
154. ***Brachioradialis*** is not a distinct muscle (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Rattus* [1] the brachioradialis is usually missing.
155. ***Supinator*** has no ulnar head. [0] In taxa of CS-0 the supinator has a single, humeral head (i.e. it mainly originates from the humerus and/or the elbow joint capsule and/or elbow ligaments). [1] *Loris*, *Nycticebus*, *Pithecia*, *Callithrix*, *Aotus*, *Saimiri*, *Macaca*, *Cercopithecus*, *Papio* and non-hylobatid hominoids usually have a distinct ulnar head of the supinator originating from the posterior portion of the ulna. *Hylobates* is coded as "?".
156. ***Extensor carpi ulnaris*** does not originate from the ulna. [0] In taxa of CS-0 the extensor carpi ulnaris originates from both the ulna and lateral epicondyle of the humerus. [1] In *Pithecia*, *Saimiri*, *Callithrix*,

- Aotus*, *Macaca*, *Cercopithecus*, *Colobus* and *Papio* the extensor carpi ulnaris originates mainly from the lateral epicondyle and does not have a direct bony origin from the ulna. *Rattus* is coded as “?”.
157. **Anconeus** is not a distinct muscle (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], in *Hylobates* [1] the anconeus is usually not present as a distinct muscle.
158. **Extensor digiti quarti** is not a distinct muscle. Contrary to *Rattus* [0], in the other taxa included in this study [1] the extensor digiti quarti is completely fused with the so-called ‘extensor digiti quinti proprius’, the two fused muscles forming the extensor digiti minimi, which often inserts onto digits 4 and 5, but may insert instead onto digits 3-5, or to digit 5 only (see characters below).
159. **Extensor digiti minimi** inserts onto digit 5 only. [0] In taxa of CS-0 the extensor digiti minimi (or the extensor digiti quarti plus the ‘extensor digiti quinti proprius’, in *Rattus*) inserts onto two or more digits - usually onto digits 4 and 5, but sometimes also onto digit 3, see character below. [1] In *Loris*, *Nycticebus*, *Hylobates*, *Gorilla*, *Pan* and modern humans the extensor digiti minimi usually inserts onto digit 5 only.
160. **Extensor digiti minimi** is partially inserted onto digit 3 (AUTAPOMORPHY). Contrary to taxa of CS-0 [0], *Cynocephalus* [1] exhibits a peculiar condition in which the extensor digiti minimi inserts onto digit 3 (as well as onto digits 4 and 5; see characters above).
161. **Extensor digiti minimi** originates from the radius (AUTAPOMORPHY). [0] In taxa of CS-0 the extensor digiti minimi (or the extensor digiti quarti plus the ‘extensor digiti quinti proprius’, in *Rattus*) has a bony origin from the lateral epicondyle of the humerus and/or, less often, from the ulna, but usually not from the radius. [1] In *Cynocephalus* the extensor digiti minimi has a bony origin from the lateral epicondyle but also from the radius.
162. **Extensor indicis** usually inserts onto digits 1-3, digits 2-4 or digit 2 only (unordered multistate character). [0] In taxa of CS-0 the extensor indicis usually inserts onto digits 2 and 3. [1] In *Cynocephalus* the muscle is commonly inserted onto digits 1, 2 and 3. [2] In *Aotus*, *Saimiri*, *Pithecia*, *Callithrix* and *Hylobates* the muscle is commonly inserted onto digits 2, 3 and 4. [3] In *Gorilla*, *Pan* and modern humans the muscle is commonly inserted onto digit 2 only. *Lemur* and *Propithecus* are coded as “?”.
163. **Extensor pollicis longus** is deeply blended with the **extensor indicis**. Contrary to taxa of CS-0 [0], in *Tupaia*, *Aotus*, *Callithrix*, *Pithecia*, *Saimiri*, and *Colobus* [1] the extensor pollicis longus is usually deeply blended with the extensor indicis, forming a mainly undivided fleshy belly (which is often designated as ‘extensor digitorum profundus’).
164. **Extensor pollicis longus** plus **extensor indicis** send two tendons to digit 2. Within the tendons of the extensor pollicis longus and of the extensor indicis only one usually goes, in taxa of CS-0 [0], to digit 2 (usually, one of the tendons of the extensor indicis). In *Saimiri*, *Callithrix*, *Aotus*, *Pithecia*, and *Colobus* [1] there are often two tendons going to digit 2, i.e. contrary to taxa of CS-0, in these genera the extensor pollicis longus sends a tendon not only to digit 1, but also to digit 2 (the other tendon that goes to digit 2 being part of the extensor indicis). *Tarsius* is coded as “?”.
165. **Abductor pollicis longus** extends to the proximal phalanx of the thumb. Contrary to taxa of CS-0 [0], in gorillas and modern humans [1] there is usually a distal extension of the abductor pollicis longus, or of a structure differentiated from it (the extensor pollicis brevis, in modern humans: see character below), to the proximal phalanx of the thumb. *Rattus* and *Cynocephalus* are coded as “?”.
166. **Extensor pollicis brevis** is a distinct muscle. Contrary to taxa of CS-0 [0], in modern humans and *Hylobates* [1] the extensor pollicis brevis is usually present as a distinct muscle.