Pairwise difference analysis in modern human origins research

Pairwise difference analysis is a phenetic method that groups taxa on the basis of the number of differences they exhibit. Recently, pairwise difference analysis has been used to investigate the phylogenetic relationships of hominid fossils at the centre of the modern human origins debate. It has been argued that the results of these analyses disprove the African replacement model of modern human origins, and support instead its competitor, the multiregional evolution model. However, this inference is problematic because the ability of pairwise difference analysis to recover phylogenetic information from morphological data has not been demonstrated. With this in mind, we conducted pairwise difference analyses of craniodental and soft tissue evidence from a group of extant primates for which a reliable molecular phylogeny is available, the hominoids. We found that the phylogenies yielded by the pairwise difference analyses were incompatible with the molecular phylogeny for the group. Given the robustness of the molecular phylogeny, these results suggest that pairwise difference analysis cannot be relied on to generate reliable estimates of primate phylogeny from morphological data. The corollary of this is that the results of published pairwise difference analyses of hominid fossils are not informative regarding the origin of modern humans.

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Introduction

The emergence of modern humans has been the focus of considerable debate over the last 30 years (e.g., Howells, 1973; Thorne & Wolpoff, 1981, 1992; Cann et al., 1987; Brauer, 1992; Smith et al., 1989; Stringer, 1989, 1992; Wolpoff, 1989, 1992; Maddison, 1991; Aiello, 1993; Lahr, 1994; Lieberman, 1995; Hublin et al., 1996; Brauer & Stringer, 1997; Krings et al., 1997; Churchill & Smith, 2000; McBrearty & Brooks, 2000; Wolpoff et al., 2000, 2001; Clark, 2002). Currently, three models dominate the dispute: the African replacement model, the assimilation model, and the multiregional evolution model (Churchill & Smith, 2000; Stringer, 2001). The African replacement model contends that modern humans arose in Africa around 150 ka and spread from there throughout the rest of the world replacing local archaic hominids with minimal interbreeding (e.g., Stringer & Andrews, 1988; Stringer, 1989, 1992; Brauer, 1992; Brauer & Stringer, 1997). The assimilation model also posits a recent African origin for modern humans, but unlike the African replacement model it contends that regional groups of archaic hominids, such as the Neanderthals, made a significant contribution to the gene pool of living humans (Smith et al., 1989; Churchill & Smith, 2000). The multiregional evolution model is still further removed from the African replacement model. It avers that modern humans arose from archaic hominids in several areas of the Old World by way of a process of genetic exchange and local selection that operated throughout the whole of the Pleistocene (e.g., Thorne &
Wolpoff, 1981, 1992; Wolpoff, 1989, 1992; Frayer et al., 1993; Wolpoff et al., 2000). Thus, the multiregional evolution model not only argues that non-African archaic hominids made a significant contribution to the gene pool of living humans, but also discounts migration of recently evolved Africans as a significant factor in the emergence of modern humans outside of Africa.

Of the predictions that can be derived from the recent African origin, assimilation and multiregional evolution models, perhaps the most important concern the phylogenetic relationships of the non-African early modern humans. The African replacement model predicts that European, East Asian and Australasian early modern humans are more closely related to African early modern humans than they are to archaic humans in Europe, East Asia and South East Asia, respectively. The assimilation model also predicts that early modern humans from Eurasia and Australasia are most closely related to African early modern humans, but it anticipates some evidence for ancestor-descendant relationships between early modern and archaic humans outside of Africa. In contrast, the multiregional evolution model predicts that early modern humans in Europe, East Asia and Australasia are at least as closely related to European, East Asian and South East Asian archaic humans, respectively, as they are to African early modern humans.

To test these predictions, hominid palaeontologists have recently turned to a form of analysis that is used in molecular biology to address phylogenetic problems, pairwise difference analysis (Hawks et al., 2000; Kramer et al., 2001; Wolpoff et al., 2001). Pairwise difference analysis is a phenetic method that groups taxa on the basis of the number of differences they exhibit. It assumes that all taxa are related, that each difference between a pair of taxa represents a mutation, and that mutations occur at a constant rate through time. Thus, in pairwise difference analysis taxa that exhibit few differences are deemed to be more closely related than taxa that exhibit many differences because they must share a common ancestor that lived more recently. Pairwise difference analysis is widely used in molecular biology since it underpins the molecular clock (Hedrick, 2000). Pairwise difference analysis has also been applied to ancient DNA sequences in order to investigate the affinities of Neanderthal and modern human fossils (e.g., Krings et al., 1997, 1999; Ovchinnikov et al., 2000). Palaeoanthropological applications of pairwise difference analysis have focused on the number of differences between pairs of fossil specimens, and on the mean number of differences among groups of fossil specimens (Hawks et al., 2000; Kramer et al., 2001; Wolpoff et al., 2001). This is similar to the approach adopted in molecular clock applications of pairwise difference analysis, and differs from the approach adopted in pairwise difference analyses of ancient DNA. In the latter, the phylogenetic relationships of an ancient individual are assessed relative to the frequency distribution of the number of differences between all possible pairs of individuals in a large sample of extant individuals (e.g., Krings et al., 1997, 1999; Ovchinnikov et al., 2000).

Applications of pairwise difference analysis in palaeoanthropology have focused on fossils from Australia, Europe and South West Asia (Hawks et al., 2000; Kramer et al., 2001; Wolpoff et al., 2001). Hawks et al. (2000) used pairwise difference analysis to investigate the affinities of WLH-50, a modern human fossil from the Willandra Lakes area of Australia that dates to 15–13 ka. Using 16 qualitative cranial characters, they compared WLH-50 with 10 Late Pleistocene modern human fossils from Africa and South West Asia, and seven specimens from the Javanese site of Ngandong that are Pleistocene in date, and which are usually classified as Homo erectus (e.g., Rightmire, 1990). The comparisons
revealed that WLH-50 is closer to six of the seven specimens from Ngandong than to any other specimen, and is only separated from the seventh Ngandong specimen by one South West Asian specimen (Skhul 9). 

Hawks et al. (2000) inferred from this that WLH-50 is likely to be a descendant of all three groups, and that the African replacement model of modern human origins can therefore be discounted. Kramer et al. (2001) used pairwise difference analysis of 12 qualitative cranial characters to assess the phylogenetic status of Neanderthal and early modern human fossils from South West Asia. Specifically, they tested the prediction from the African replacement model that the Neanderthal specimens from Tabun and Amud should group together to the exclusion of the modern human specimens from Skhul and Qafzeh. Kramer et al. (2001) found that the prediction was not met. The mean number of differences between Tabun and the Skhul/Qafzeh crania did not differ significantly from the number of differences between Tabun and Amud. They concluded from this that the African replacement model can be discounted. Wolpoff et al. (2001) replicated the WLH-50 analysis carried out by Hawks et al. (2000) and also outlined a pairwise difference analysis that focused on the affinities of early modern human fossils from the Moravian Upper Palaeolithic site of Mladec. Based on 30 qualitative cranial characters, the latter analysis indicated that the number of differences between the Mladec crania and Neanderthal specimens from Europe and South West Asia was similar to the number of differences between the Mladec crania and early modern human specimens from South West Asia. Wolpoff et al. (2001) argued that the results of their pairwise difference analyses are in line with the multiregional evolution model of modern human origins rather than the African replacement model.

The studies in which pairwise difference analysis has been applied to hominid fossil material appear to refute the African replacement model of modern human origins and support instead its competitor, the multiregional evolution model (Hawks et al., 2000; Kramer et al., 2001; Wolpoff et al., 2001). However, while the ability of pairwise difference analysis to recover phylogenetic information from biomolecular data is well established, its ability to recover such information from morphological data has not been evaluated. As such, the inference that the pairwise difference analyses of fossil hominids undercut the African replacement model and confirm the multiregional evolution model is problematic. The results of these analyses may, as Hawks et al. (2000), Kramer et al. (2001) and Wolpoff et al. (2001) contend, disprove the African replacement model and support the multiregional evolution model. But it is also possible that pairwise difference analysis is unable to recover phylogenetic information from morphological data, in which case the results of the fossil hominid analyses are uninformative regarding the African replacement and multiregional evolution models of modern human origins.

Here we report a study in which the ability of pairwise difference analysis to recover phylogenetic information from hominid morphological data was evaluated through analyses of craniodental and soft tissue evidence from the extant hominoids. These primates have been the focus of considerable molecular phylogenetic research, and there is now widespread agreement that their phylogenetic relationships can be considered known (e.g., Ruvolo, 1997; Gagneux & Varki, 2001; Page & Goodman, 2001). Accordingly we assumed that, if the phylogenetic hypotheses yielded by pairwise difference analyses of the hominoid morphological data match the group’s molecular phylogeny (Figure 1), pairwise difference analysis can be relied on to recover phylogenetic information from primate morphological data, and the results of Hawks et al.’s
(2000), Kramer et al.’s (2001) and Wolpoff et al.’s (2001) pairwise difference analyses of fossil hominids can be considered valid. Conversely, we also assumed that, if pairwise difference analyses of the hominoid morphological data yield phylogenetic hypotheses that disagree with the group’s molecular phylogeny, pairwise difference analysis cannot be relied on to recover phylogenetic information from primate morphological data, and the results of Hawks et al.’s (2000), Kramer et al.’s (2001) and Wolpoff et al.’s (2001) fossil hominid pairwise difference analyses cannot be considered valid.

**Materials and methods**

Three datasets were employed in the study. The first comprised the states of 96 qualitative craniodental characters recorded on *Gorilla, Homo, Hylobates, Pan* and *Pongo*. This dataset was taken from Collard & Wood (2000). The character definitions and states are given in Appendix 1. The second dataset comprised the states of 171 qualitative soft tissue characters recorded on *Gorilla, Homo, Hylobates, Pan* and *Pongo*. These data were taken from Gibbs et al. (2002). The definitions and states of the characters are given in Appendix 2. The third dataset consisted of values for 129 craniodental measurements recorded on mixed sex samples of adult *Colobus, Gorilla, Homo, Pan* and *Pongo*. Seventy-seven of the measurements were recorded on 37 *Gorilla gorilla* (20 males, 17 females), 75 *H. sapiens* (40 males, 35 females), 35 *Pan troglodytes* (13 males, 22 females), 41 *Pongo pygmaeus* (20 males, 21 females) and 24 *Colobus guereza* (12 males, 12 females). The other 52 measurements were recorded on 20 *G. gorilla* (ten males, ten females), 20 *H. sapiens* (ten males, ten females), 20 *P. troglodytes* (ten males, ten females), 20 *P. pygmaeus* (ten males, ten females) and 20 *C. guereza* (ten males, ten females). These data were also taken from Collard & Wood (2000). Details of the measurements are given in Appendix 3. Cranial measurements were rounded up to the nearest 1 mm, and dental measurements to the nearest 0.1 mm.

Four analyses were carried out to assess the ability of pairwise difference analysis to recover phylogenetic information from primate morphological data. The first and second analyses involved the qualitative craniodental and soft tissue datasets, respectively. In both analyses, the states exhibited by the taxa were compared on a pairwise basis and the number of differences
between each pair recorded in a matrix. Thereafter, a nearest-neighbour phylogeny was constructed from the matrix of differences by sequentially linking taxa that returned the smallest number of differences in the pairwise comparisons. This method of clustering was chosen as it best approximates the procedure used by Hawks et al. (2000), Kramer et al. (2001) and Wolpoff et al. (2001). Lastly, the morphological phylogeny was judged against the consensus molecular phylogeny for the extant hominoids, which was assumed to accurately represent the relationships among them (Ruvolo, 1997; Gagneux & Varki, 2001; Page & Goodman, 2001). The third analysis focussed on the quantitative craniodental data. The data were adjusted to counteract the confounding effects of the size differences among the taxa. This was accomplished by dividing each value by the geometric mean of all the values for the appropriate specimen (Darroch & Mosiman, 1985; Jungers et al., 1995). Next, the significance of the differences between the means was evaluated on a pairwise basis using the two-tailed t-test, and the number of significant differences recorded in a matrix. Subsequently, a nearest neighbour phylogeny was constructed and then judged against the hominoid molecular phylogeny. In the fourth analysis, the 96-character qualitative craniodental and 171-character soft tissue datasets were combined. Next, the states exhibited by the taxa were compared on a pairwise basis and the number of differences between each pair recorded in a matrix. Thereafter, a nearest neighbour phylogeny was constructed and then judged against the hominoid molecular phylogeny. Lastly, the effect of the small number of uncertain and polymorphic character states in the first two datasets was assessed. This was accomplished by comparing the results of analyses in which the ambiguous character states were set to 0 with the results of analyses in which the ambiguous character states were set to 1. All the analyses were performed in Excel 2001.

### Results

Four analyses were conducted in order to assess the ability of pairwise difference analysis to recover phylogenetic information from primate morphological data. In the first analysis, pairwise difference analysis was applied to a dataset comprised of the states of 96 qualitative characters recorded on Gorilla, Homo, Hylobates, Pan and Pongo. The number of differences among the taxa is presented in Table 1, and the phylogeny derived from the number of differences is shown in Figure 2. The latter is incompatible with the hominoid molecular phylogeny (Figure 1), since it suggests that Gorilla and Pan share a common ancestor to the exclusion of Homo, Hylobates and Pongo. It also differs from the molecular phylogeny in suggesting that Gorilla, Homo and Pan share an ancestor to the exclusion of Hylobates and Pongo, and that Gorilla, Homo, Hylobates and Pan share an ancestor to the exclusion of Pongo. The analyses conducted to examine the effects of the uncertain and polymorphic character states (characters 63, 64, 85 and 94) produced phylogenies with the same topology as the phylogeny obtained in the analysis of the unaltered data. The first analysis therefore suggested that pairwise difference analysis is unable to recover

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<th>Homo</th>
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<tr>
<td>Gorilla</td>
<td>53</td>
<td>58</td>
<td>20</td>
<td>62</td>
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<tr>
<td>Homo</td>
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<td>42</td>
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<tr>
<td>Pan</td>
<td>63</td>
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Each value represents the number of morphological differences between a pair of taxa.
phylogenetic information from primate morphological data.

In the second analysis, pairwise difference analysis was applied to a dataset consisting of the states of 171 qualitative soft tissue characters recorded on Gorilla, Homo, Hylobates, Pan and Pongo. Table 2 shows the number of differences among the taxa, and Figure 3 presents the phylogeny derived from the number of differences. The phylogeny is consistent with the hominoid molecular phylogeny (Figure 1) in that it suggests that Homo and Pan share a common ancestor to the exclusion of Gorilla, Hylobates and Pongo. However, it differs from the molecular phylogeny in suggesting that Hylobates and Pongo share an ancestor to the exclusion of Gorilla, Homo and Pan. It also differs from the molecular phylogeny in suggesting that Gorilla is equally closely related to the (Homo, Pan) clade and the (Hylobates, Pongo) clade. One of the analyses undertaken to assess the effect of the missing state for Hylobates for character 18 returned a phylogeny with the same topology as the unaltered data. The other analysis returned a phylogeny that was even more incongruent with the molecular phylogeny. It suggested that Hylobates and Pongo share an ancestor to the exclusion of Gorilla, Homo and Pan, that Gorilla shares an ancestor with Hylobates and Pongo to the exclusion of Homo and Pan, and that Homo and Pan share an ancestor to the exclusion of Gorilla, Hylobates and Pongo. Hence, the second analysis also suggested that pairwise difference analysis is unable to recover phylogenetic information from primate morphological data.

In the third analysis, pairwise difference analysis was applied to a dataset consisting of the states of 129 quantitative craniodental

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<th>Pan</th>
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<td>99</td>
<td>100</td>
<td>108</td>
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<tr>
<td>Homo</td>
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<td>Hylobates</td>
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<tr>
<td>Pan</td>
<td></td>
<td>115</td>
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Each value represents the number of morphological differences between a pair of taxa.

Figure 2. Phylogeny returned by pairwise difference analysis of 96 qualitative craniodental characters.

Figure 3. Phylogeny returned by pairwise difference analysis of 171 soft tissue characters.
characters recorded on *Colobus*, *Gorilla*, *Homo*, *Pan* and *Pongo*. The number of differences among the taxa is shown in Table 3, and the phylogeny derived from the number of differences is presented in Figure 4. The phylogeny differs considerably from the molecular phylogeny (Figure 1). Most notably it suggests that the Old World monkey genus *Colobus* shares a common ancestor with three of the hominoid genera, *Gorilla*, *Pan* and *Pongo*, to the exclusion of the fourth hominoid genus, *Homo*. In addition, the craniometric phylogeny suggests that *Pan* and *Pongo* share a common ancestor to the exclusion of *Gorilla*. Thus, the third analysis, like the previous two analyses, suggests pairwise difference analysis is unable to recover phylogenetic information from primate morphological data.

In order to assess the ability of pairwise difference analysis to recover phylogenetic information from primate morphological data, four analyses were carried out. In each analysis, pairwise difference analysis was applied to a hominoid morphological dataset, a nearest-neighbour phylogeny was constructed from the results of the pairwise difference analysis, and then the morphological phylogeny was judged against the group’s molecular phylogeny. In all four analyses the phylogenetic hypotheses returned by pairwise difference analysis were incompatible with the molecular phylogeny for the extant hominoids.

Given the robustness of the hominoid molecular phylogeny (*Ruvolo*, 1997; *Gagneux* & *Varki*, 2001; *Page* & *Goodman*, 2001), these results indicate that pairwise difference analysis cannot be relied on to recover phylogenetic information from primate morphological datasets. It is possible that future studies will show that pairwise difference analysis is able to recover phylogenetic information from some datasets, but the results of our analyses indicate that it is unable to recover phylogenetic information from all primate morphological datasets. Thus, it cannot automatically be assumed that a phylogeny yielded by a pairwise difference analysis of primate morphological data is accurate. The corollary of this is that the results of the pairwise difference analyses

### Table 3 Results of pairwise difference analysis of quantitative craniodental dataset

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<th></th>
<th>Pongo</th>
<th>Gorilla</th>
<th>Pan</th>
<th>Homo</th>
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<tr>
<td>Colobus</td>
<td>118</td>
<td>121</td>
<td>111</td>
<td>114</td>
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<td>Pongo</td>
<td>95</td>
<td>86</td>
<td>124</td>
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<tr>
<td>Gorilla</td>
<td>104</td>
<td>121</td>
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<tr>
<td>Pan</td>
<td>119</td>
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Each value represents the number of morphological differences between a pair of taxa.
of fossil hominids carried out by Hawks et al. (2000), Kramer et al. (2001) and Wolpoфф et al. (2001) are uninformative regarding modern human origins. They may refute the African replacement model and support the multiregional evolution model, as Hawks et al. (2000), Kramer et al. (2001) and Wolpoфф et al. (2001) contend, but it may also be the case that, like the phylogenetic hypotheses we obtained using pairwise difference analysis, the fossil hominid phylogenetic hypotheses are inaccurate. Since there is no way of determining which of these possibilities is correct, the results of Hawks et al.’s (2000), Kramer et al.’s (2001) and Wolpoфф et al.’s (2001) pairwise difference analyses neither refute the African replacement nor support the multiregional evolution model.

Three potential criticisms of our analyses could undermine the foregoing conclusions regarding the reliability of pairwise difference analysis of primate morphological data, and the implications of the results of the fossil hominid pairwise difference analyses carried out by Hawks et al. (2000), Kramer et al. (2001) and Wolpoфф et al. (2001). The first is that our analyses focused on the phylogenetic relationships among genera whereas the fossil hominid analyses concentrated on the phylogenetic relationships among individual fossils and groups of fossils. Thus, it could be argued that it is inappropriate to conclude from our results that published pairwise difference analyses of fossil hominids are incapable of refuting or supporting models of modern human origins. This criticism would perhaps be valid if the ease with which phylogenetic relationships can be reconstructed were inversely correlated with taxonomic level. But this does not seem to be the case. On the contrary, it is widely assumed that intraspecific phylogenetic relationships are more difficult to reconstruct than interspecific phylogenetic relationships, which in turn are more difficult to reconstruct than the phylogenetic relationships among supraspecific taxa (e.g., Trinkaus, 1990, 1992; Lieberman, 1995; Collard & Wood, 2000). As such, we believe the results of our analyses are relevant to the reliability of the results of published fossil hominid pairwise difference analyses.

### Table 4 Results of pairwise difference analysis of qualitative craniodental and soft tissue dataset

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<tr>
<td>Gorilla</td>
<td>160</td>
<td>157</td>
<td>120</td>
<td>170</td>
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<tr>
<td>Homo</td>
<td>179</td>
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<td>Hylobates</td>
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<tr>
<td>Pan</td>
<td></td>
<td></td>
<td>178</td>
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</table>

Each value represents the number of morphological differences between a pair of taxa.

Figure 4. Phylogeny returned by pairwise difference analysis of 129 quantitative craniodental characters.
The second potential criticism concerns the type of morphological data employed in our analyses. It has been suggested recently that craniodental characters are unreliable for reconstructing the phylogenetic relationships among higher primate species and genera (Hartman, 1988; Harrison, 1993; Pilbeam, 1996; Collard & Wood, 2000). Thus, it could be argued that the incongruence between our morphological phylogenies and the molecular phylogeny reflect the limitations of the data rather than the limitations of pairwise difference analysis. However, this argument cannot be sustained. Gibbs and colleagues’ (2000, 2002) cladistic analyses of the hominoid soft tissue dataset we employed yielded a well-supported phylogeny with the same topology as the hominoid molecular phylogeny (Figure 1). In contrast, the pairwise difference analysis of the data reported here returned a phylogeny that disagrees with the hominoid molecular phylogeny regarding the relationships of Gorilla, Hylobates and Pongo (Figure 3). This strongly supports the inference that pairwise difference analysis is not useful for estimating phylogenetic relationships among primate species and genera. Moreover, even if it is assumed that the results of the analyses in which pairwise difference analysis was applied to hominoid craniodental data reflect the limitations of such data, there is still no reason to consider the results of the pairwise difference analyses carried out by Hawks et al. (2000), Kramer et al. (2001) and Wolpoff et al. (2001) to be informative regarding modern human origins, since they are also based on higher primate craniodental characteristics.

The third potential criticism is that our datasets are inadequate as far as sample size and character number are concerned. We reject this criticism on two counts, especially as it relates to our conclusion that the results of the pairwise difference analyses carried out by Hawks et al. (2000), Kramer et al. (2001) and Wolpoff et al. (2001) are incapable of refuting or supporting any model of modern human origins. First, we used many more characters than Hawks et al. (2000), Kramer et al. (2001) and Wolpoff et al. (2001). We employed between 96 and 267 characters, while Hawks et al. (2000) used 16, Kramer et al. (2001) used 12, and Wolpoff et al. (2001) used 30. Second, while our qualitative datasets are based on observations of relatively small numbers of individuals (Collard & Wood, 2000; Gibbs et al., 2002), our quantitative data are derived from samples of specimens that are considerably larger than those employed by Hawks et al. (2000), Kramer et al. (2001) and Wolpoff et al. (2001) in their fossil hominid pairwise difference analyses. Our quantitative dataset comprises values for between 20 and 75 specimens per genus.
whereas the datasets employed by Hawks et al. (2000), Kramer et al. (2001) and Woloff et al. (2001) include information on 36 specimens in total. It is possible that the number of characters and individuals we employed are insufficient for pairwise difference analysis to be able recover the correct phylogeny. However, if our results are problematic due to an insufficient number of characters and/or number of specimens having been examined, the same must hold for the results of Hawks et al. (2000), Kramer et al. (2001) and Woloff et al. (2001), in which case our conclusion that the latter are uninformative regarding modern human origins still stands.

Thus, the potential criticisms of our study can either be discounted or shown to be less significant in relation to our analyses than to the pairwise difference analyses of fossil hominids conducted by Hawks et al. (2000), Kramer et al. (2001) and Woloff et al. (2001). We believe, therefore, that there is no reason to reject the conclusion that pairwise difference analysis cannot be relied on to recover phylogenetic information from primate morphological datasets. We also believe that there is no reason to reject the conclusion that the results of the pairwise difference analyses of fossil hominids carried out by Hawks et al. (2000), Kramer et al. (2001) and Woloff et al. (2001) are uninformative regarding modern human origins. It is important to note that these conclusions do not lend support to any model of modern human origins. It does not follow from the failure of our analyses to support the conclusions of Hawks et al. (2000), Kramer et al. (2001) and Woloff et al. (2001) that the African replacement model is correct and the multiregional evolution model incorrect. Rather the results of our analyses simply mean that the merits of the African replacement and multiregional evolution models of modern human origins should be assessed without reference to Hawks et al.’s (2000), Kramer et al.’s (2001) and Woloff et al.’s (2001) pairwise difference analyses of fossil hominids.

Conclusions

In this study we sought to evaluate recent claims that pairwise difference analyses of hominid fossils disprove the African replacement model of modern human origins, and support instead its competitor, the multiregional evolution model (Hawks et al., 2000; Kramer et al., 2001; Woloff et al., 2001). To do so, we conducted four pairwise difference analyses of craniodental and morphological data from a group of extant primates for which a reliable molecular phylogeny is available, the hominoids. In each analysis, pairwise difference analysis was applied to a morphological dataset, a phylogeny was constructed by sequentially linking taxa that returned the smallest number of differences in the pairwise difference analysis, and then the morphological phylogeny was judged against the group’s molecular phylogeny. In all four analyses the phylogenetic hypotheses returned by pairwise difference analysis were incompatible with the molecular phylogeny for the extant hominoids.

Given the robustness of the hominoid molecular phylogeny, the results of our analyses indicate that pairwise difference analysis cannot be relied on to recover phylogenetic information from all primate morphological datasets. The corollary of this is that the results of the pairwise difference analyses of fossil hominids carried out by Hawks et al. (2000), Kramer et al. (2001) and Woloff et al. (2001) are incapable of refuting or supporting any model of modern human origins. Thus, contrary to the claims of Hawks et al. (2000), Kramer et al. (2001) and Woloff et al. (2001), the results of their pairwise difference analyses of fossil hominids do not refute the African replacement model and support the multiregional evolution model.
Acknowledgements

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References


Appendix 1. Details of the 96 qualitative craniodental characters used in the study

The description of each character is followed by the key to the character states (“States”) and the distribution of character states among the taxa (“Dist”). Further details, including the references for allocating the character states to the taxa, can be found in Collard & Wood (2000).

1. Depth of subarcuate fossa
   States: (0) deep; (1) moderately deep to shallow; (2) very shallow to nonexistent.
   Dist.: _Homo_ 2; _Pan_ 2; _Gorilla_ 2; _Pongo_ 2; _Hylobates_ 1; _Colobus_ 0.

2. Morphology of the mandibular symphysis
   States: (1) elongated and spout-like with an angle of 150°–145°; (2) symphysis with an angle of 137°–115°; (3) angle of mandibular symphysis (excluding the simian shelf) to horizontal ramus is narrow, approaching vertical when observed dorsally and laterally, with a mandibular symphysis angle of about 100°–90° or less.
   Dist.: _Homo_ 3; _Pan_ 2; _Gorilla_ 1; _Pongo_ 2; _Hylobates_ 2; _Colobus_ 1.

3. Distinctiveness of angular process of mandible
   States: (0) distinct, with posterior projection; (1) not distinct.
   Dist.: _Homo_ 1; _Pan_ 1; _Gorilla_ 1; _Pongo_ 1; _Hylobates_ 0; _Colobus_ 1.

4. Direction of incisive (anterior palatine) foramen
   States: (0) opening is directed dorsoventrally as in most mammals and the observer can see through the foramen; (1) foramen is directed diagonally, from anterior–ventral to posterior–dorsal, leads to a tube-like structure, and one cannot see through the foramina.
   Dist.: _Homo_ 1; _Pan_ 1; _Gorilla_ 1; _Pongo_ 1; _Hylobates_ 0; _Colobus_ 0.
5. **Carotid canal morphology when viewed from ventral side of cranium**

   States: (1) canal perforates bulla away from basicranium and is clearly within it, opening of canal is directed medially, ventrally or ventro-medially, but the imaginary lines (one from each side) which emerge from these openings do not cross at the foramen magnum, or cross at its anterior border at the level of the occipital condyles; (2) canal perforates bulla away from basicranium and is clearly within it, opening is directed postero-medially and the imaginary lines which emerge from these openings cross the foramen magnum posterior to the occipital condyles, or caudal to the foramen magnum itself.

   Dist.: Homo 1; Pan 1; Gorilla 1; Pongo 1; Hylobates 2; Colobus 1.

6. **Size of upper first incisor relative to upper second incisor**

   States: (0) about the same size; (1) enlarged; (2) much enlarged.

   Dist.: Homo 1; Pan 1; Gorilla 1; Pongo 2; Hylobates 0; Colobus 0.

7. **Honing in males (back of upper canine sharpens against third lower premolar)**

   States: (1) present, i.e., P₃ bilaterally compressed (sectorial) and modified for honing on C₁, P₃ is larger than P₄ especially mesiodistally, also may involve honing C₁ on C₃; (2) honing reduced, P₃ slightly buccolingually compressed, P₃ is larger than P₄ especially mesiodistally; (3) honing further reduced, P₃ about the same size as P₄ in length in occlusal view.

   Dist.: Homo 2; Pan 2; Gorilla 1; Pongo 1; Hylobates 1; Colobus 0.

8. **Interorbital pillar width**

   States: (0) wide; (1) narrow.

   Dist.: Homo 0; Pan 0; Gorilla 1; Pongo 1; Hylobates 0; Colobus 0.

9. **Depth of middle ear**

   States: (0) shallow; (1) deepened, more than 8.5 mm.

   Dist.: Homo 1; Pan 1; Gorilla 1; Pongo 0; Hylobates 0; Colobus 0.

10. **Axis of ear bones**

    States: (0) acute angle; (1) right angle or more.

    Dist.: Homo 0; Pan 0; Gorilla 1; Pongo 1; Hylobates 1; Colobus 0.

11. **Area of inner ear**

    States: (0) low, <50 mm²; (1) increased, >50 mm².

    Dist.: Homo 1; Pan 1; Gorilla 1; Pongo 0; Hylobates 0; Colobus 0.

12. **Klinorhynch (a deep foreshortened facial skeleton which bends downward with respect to the cranial base)**

    States: (0) airorynch or straight; (1) more klinorhynch; (2) strongly klinorhynch.

    Dist.: Homo 2; Pan 2; Gorilla 2; Pongo 0; Hylobates 1; Colobus 0.

13. **Frontozygomatic suture**

    States: (0) vertical; (1) medially directed.

    Dist.: Homo 0; Pan 0; Gorilla 0; Pongo 1; Hylobates 0; Colobus 0.

14. **Relative height of upper face**

    States: (0) high, index about 70; (1) reduced.

    Dist.: Homo 0; Pan 1; Gorilla 0; Pongo 0; Hylobates 1; Colobus 0.

15. **Facial index (upper face height as a percentage of facial breadth)**

    States: (0) low, index about 50; (1) increased.

    Dist.: Homo 0; Pan 1; Gorilla 1; Pongo 1; Hylobates 0; Colobus 0.

16. **Height of mandibular symphysis relative to length of the lower toothrow**

    States: (0) low, its height about 60% of toothrow length; (1) deepened, at least 75% of tooth row length.

    Dist.: Homo 0; Pan 1; Gorilla 1; Pongo 1; Hylobates 0; Colobus 1.
17. Presence/absence of frontal sinus
States: (0) absent; (1) present.
Dist.: Homo 1; Pan 1; Gorilla 1; Pongo 0; Hylobates 0; Colobus 0.

18. Pyriform aperture
States: (0) narrow; (1) widened; (2) very wide.
Dist.: Homo 2; Pan 2; Gorilla 2; Pongo 1; Hylobates 2; Colobus 0.

19. Position of infraorbital foramina relative to zygomatic suture
States: (0) close to suture; (1) further from suture.
Dist.: Homo 0; Pan 0; Gorilla 0; Pongo 1; Hylobates 0; Colobus 1.

20. Orientation of zygomatic bone
States: (0) more frontally; (1) more superolaterally; (2) still further superolaterally.
Dist.: Homo 2; Pan 2; Gorilla 2; Pongo 1; Hylobates 0; Colobus 1.

21. Frontal bone
States: (0) flat; (1) more convex; (2) strongly convex.
Dist.: Homo 2; Pan 0; Gorilla 0; Pongo 2; Hylobates 1; Colobus 2.

22. Glabella prominence
States: (0) strong; (1) reduced; (2) absent.
Dist.: Homo 0; Pan 0; Gorilla 0; Pongo 1; Hylobates 2; Colobus 0.

23. Number of incisive foramina
States: (0) double, i.e., one on each side of the midline; (1) single, confluence of two foramina, at least close to the surface.
Dist.: Homo 1; Pan 0; Gorilla 0; Pongo 1; Hylobates 0; Colobus 0.

24. Maxillary sinus
States: (0) small; (1) expanded.
Dist.: Homo 0; Pan 0; Gorilla 0; Pongo 1; Hylobates 0; Colobus 0.

25. Supraorbital development
States: (0) weak; (1) more marked; (2) torus-like.
Dist.: Homo 2; Pan 2; Gorilla 2; Pongo 0; Hylobates 1; Colobus 1.

26. Supraorbital contour
States: (0) arched; (1) less arched.
Dist.: Homo 0; Pan 0; Gorilla 1; Pongo 0; Hylobates 0; Colobus 1.

27. Orbits
States: (0) as wide as high; (1) high oval.
Dist.: Homo 0; Pan 0; Gorilla 0; Pongo 1; Hylobates 0; Colobus 0.

28. Supraorbital trigon
States: (0) not developed; (1) developed.
Dist.: Homo 0; Pan 1; Gorilla 1; Pongo 0; Hylobates 0; Colobus 1.

29. Nasal width
States: (0) broad; (1) reduced.
Dist.: Homo 0; Pan 0; Gorilla 0; Pongo 1; Hylobates 0; Colobus 0.

30. Length of nasals
States: (0) long; (1) shortened.
Dist.: Homo 1; Pan 0; Gorilla 0; Pongo 0; Hylobates 1; Colobus 1.

31. Size of zygomatic foramina
States: (0) very small; (1) enlarged.
Dist.: Homo 0; Pan 0; Gorilla 0; Pongo 1; Hylobates 0; Colobus 0.

32. Position of zygomatic foramina
States: (0) at or below plane of orbital rim; (1) above plane of orbital rim.
Dist.: Homo 0; Pan 0; Gorilla 0; Pongo 1; Hylobates 0; Colobus 1.

33. Size of incisive foramina
States: (0) large; (1) reduced in size; (2) tiny.
Dist.: Homo 1; Pan 1; Gorilla 1; Pongo 2; Hylobates 0; Colobus 0.
34. Size and shape of palatine foramina  
   States: (0) large and wide; (1) small and narrow.  
   Dist.: Homo 0; Pan 0; Gorilla 0; Pongo 1; Hylobates 0; Colobus 0.

35. Premaxillary suture in adult  
   States: (0) patent; (1) obliterated.  
   Dist.: Homo 1; Pan 1; Gorilla 0; Pongo 0; Hylobates 0; Colobus 0.

36. Foramen lacerum medium  
   States: (0) absent; (1) present.  
   Dist.: Homo 1; Pan 0; Gorilla 0; Pongo 1; Hylobates 0; Colobus 0.

37. Posterior convergence of temporal lines  
   States: (0) converge posteriorly; (1) do not converge.  
   Dist.: Homo 1; Pan 0; Gorilla 0; Pongo 1; Hylobates 0; Colobus 0.

38. Mesial groove on male canine  
   States: (0) extends on to root; (1) present; (2) absent.  
   Dist.: Homo 1; Pan 1; Gorilla 1; Pongo 2; Hylobates 0; Colobus 0.

39. Relative height of male canine  
   States: (0) high relative to mesiodistal length; (1) lower relative to mesiodistal length.  
   Dist.: Homo 1; Pan 1; Gorilla 1; Pongo 1; Hylobates 0; Colobus 0.

40. Upper l2 occlusal edge  
   States: (0) slopes distally; (1) does not slope distally.  
   Dist.: Homo 1; Pan 1; Gorilla 0; Pongo 0; Hylobates 0; Colobus 0.

41. Robusticity of canines  
   States: (0) slender; (1) more robust.  
   Dist.: Homo 1; Pan 1; Gorilla 1; Pongo 0; Hylobates 0; Colobus 0.

42. Basal keel of lower canines  
   States: (0) present; (1) absent.  
   Dist.: Homo 1; Pan 1; Gorilla 0; Pongo 0; Hylobates 0; Colobus 0.

43. Basal area of paracone of upper premolars  
   States: (0) subequal to protocone; (1) smaller than protocone.  
   Dist.: Homo 0; Pan 0; Gorilla 0; Pongo 1; Hylobates 1; Colobus 1.

44. Molar cingulum  
   States: (0) prominent, shelf-like; (1) reduced, incomplete, (2) fragmented or absent.  
   Dist.: Homo 2; Pan 2; Gorilla 0; Pongo 0; Hylobates 0; Colobus 1.

45. Protoconid apex on lower dP3  
   States: (0) more lingual from the median axis; (1) truncated buccally from the median axis.  
   Dist.: Homo 1; Pan 0; Gorilla 0; Pongo 1; Hylobates 0; Colobus 0.

46. Metaconid of lower dP3  
   States: (0) present; (1) absent.  
   Dist.: Homo 0; Pan 1; Gorilla 1; Pongo 0; Hylobates 0; Colobus 0.

47. Protocristid of lower dP3  
   States: (0) aligned with tooth mesiodistal axis; (1) angled.  
   Dist.: Homo 0; Pan 1; Gorilla 0; Pongo 0; Hylobates 0; Colobus 0.

48. Talonid basin of lower dP3  
   States: (0) open distally; (1) closed.  
   Dist.: Homo 1; Pan 0; Gorilla 0; Pongo 1; Hylobates 0; Colobus 0.

49. Metaconid of lower dP4  
   States: (0) subequal to protoconid; (1) increased relative to protoconid on lower dP4.  
   Dist.: Homo 0; Pan 1; Gorilla 1; Pongo 0; Hylobates 0; Colobus 0.

50. Crista obliqua on lower dP4  
   States: (0) does not reach protoconid apex; (1) reaches protoconid apex.  
   Dist.: Homo 1; Pan 0; Gorilla 0; Pongo 1; Hylobates 1; Colobus 0.
51. **Talonid basin on lower dP4**
   States: (0) open distally; (1) closed.
   Dist.: Homo 1; Pan 0; Gorilla 0; Pongo 1; Hylobates 1; Colobus ?.

52. **Protocone of upper dP3, in crown view**
   States: (0) larger than paracone; (1) smaller than paracone.
   Dist.: Homo 1; Pan 0; Gorilla 0; Pongo 1; Hylobates 0; Colobus ?.

53. **Preprotocrista of upper dP4**
   States: (0) weak; (1) more developed.
   Dist.: Homo 1; Pan 1; Gorilla 1; Pongo 1; Hylobates 0; Colobus ?.

54. **Postprotocrista of upper dP4**
   States: (0) poor; (1) more developed; (2) still more developed.
   Dist.: Homo 2; Pan 2; Gorilla 2; Pongo 1; Hylobates 1; Colobus 0.

55. **Protocristid grooves of molars**
   States: (0) prominent; (1) barely visible.
   Dist.: Homo 0; Pan 1; Gorilla 0; Pongo 1; Hylobates 1; Colobus 0.

56. **Lingual marginal ridges of molars**
   States: (0) hardly appreciable; (1) more prominent; (2) very prominent.
   Dist.: Homo 1; Pan 1; Gorilla 2; Pongo 1; Hylobates 1; Colobus 0.

57. **Thickness of molar enamel**
   States: (0) thin; (1) increased thickness; (2) very thick.
   Dist.: Homo 2; Pan 0; Gorilla 0; Pongo 1; Hylobates 0; Colobus ?.

58. **Proportion of Pattern 3 enamel**
   States: (0) high; (1) reduced; (2) very reduced.
   Dist.: Homo 0; Pan 2; Gorilla 2; Pongo 1; Hylobates 0; Colobus ?.

59. **Insertion of genioglossal**
   States: (0) above inferior transverse torus of internal (or posterior) mandibular symphysis; (1) shifted to inferior transverse torus.
   Dist.: Homo 0; Pan 1; Gorilla 1; Pongo 1; Hylobates 0; Colobus 0.

60. **Insertion of geniohyoideus**
   States: (0) basally on inferior transverse torus; (1) higher on inferior transverse torus; (2) above inferior transverse torus.
   Dist.: Homo 2; Pan 2; Gorilla 1; Pongo 0; Hylobates 1; Colobus 0.

61. **Insertion of digastric**
   States: (0) posterior to inferior transverse torus; (1) inferior transverse torus; (2) not on symphysis.
   Dist.: Homo 1; Pan 1; Gorilla 1; Pongo 2; Hylobates 0; Colobus 0.

62. **Encephalization**
   States: (0) low, <1.2; (1) increased, >1.2-1.9; (2) high >1.9.
   Dist.: Homo 2; Pan 1; Gorilla 0; Pongo 1; Hylobates 2; Colobus 0.

63. **Retroarticular canal**
   States: (0) absent; (1) present.
   Dist.: Homo 0; Pan 0; Gorilla 0; Pongo 1; Hylobates ?; Colobus ?.

64. **Condylar canal**
   States: (0) absent; (1) present.
   Dist.: Homo 1; Pan 1; Gorilla 1; Pongo 0; Hylobates ?; Colobus ?.

65. **Incisive fossa**
   States: (0) absent; (1) deep; (2) extends through palate.
   Dist.: Homo 1; Pan 1; Gorilla 1; Pongo 0; Hylobates 2; Colobus ?.

66. **Molar dentine horns**
   States: (0) high; (1) low.
   Dist.: Homo 0; Pan 0; Gorilla 0; Pongo 1; Hylobates 0; Colobus ?.
67. **Molar enamel wrinkling**  
States: (0) smooth or slight wrinkling; (1) deep secondary wrinkling.  
Dist.: *Homo* 0; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* ?.

68. **Postorbital sulcus**  
States: (0) absent; (1) present.  
Dist.: *Homo* 1; *Pan* 1; *Gorilla* 1; *Pongo* 0; *Hylobates* 0; *Colobus* ?.

69. **Ethmoid-lacrimal contact**  
States: (0) long, 100%; (1) short, 40–90%.  
Dist.: *Homo* 0; *Pan* 1; *Gorilla* 1; *Pongo* 0; *Hylobates* 0; *Colobus* ?.

70. **Fronto-maxillary contact in orbits**  
States: (0) no contact; (1) contact, 30–50%.  
Dist.: *Homo* 0; *Pan* 1; *Gorilla* 1; *Pongo* 0; *Hylobates* 0; *Colobus* ?.

71. **Nasal floor morphology**  
States: (0) nasal floor stepped; (1) nasal floor unstepped.  
Dist.: *Homo* 0; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* ?.

72. **Palatine fenestrae reduced in size**  
States: (0) no; (1) yes.  
Dist.: *Homo* 1; *Pan* 1; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* ?.

73. **Cheek tooth height**  
States: (0) low; (1) medium; (2) medium-high; (3) high.  
Dist.: *Homo* 0; *Pan* 2; *Gorilla* 3; *Pongo* 0; *Hylobates* 1; *Colobus* 0.

74. **Lower M3 smaller than lower M2**  
States: (0) no; (1) yes.  
Dist.: *Homo* 1; *Pan* 1; *Gorilla* 0; *Pongo* 1; *Hylobates* 1; *Colobus* ?.

75. **Number of zygomatic foramina**  
States: (0) 1–2; (1) 1–2+.  
Dist.: *Homo* 0; *Pan* 0; *Gorilla* 1; *Pongo* 1; *Hylobates* 0; *Colobus* ?.

76. **Post talonid basin**  
States: (0) absent; (1) small; (2) narrow.  
Dist.: *Homo* 1; *Pan* 2; *Gorilla* 2; *Pongo* 2; *Hylobates* 0; *Colobus* ?.

77. **Relative depth of mandible**  
States: (0) deep/moderate; (1) moderate; (2) shallow.  
Dist.: *Homo* 1; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 2; *Colobus* 0.

78. **Mandibular shape**  
States: (0) shallows mesially/constant; (1) constant; (2) deepens.  
Dist.: *Homo* 1; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 2; *Colobus* 0.

79. **Ethmo-sphenoid contact**  
States: (0) none/very short, 0–39%; (1) short, 40–90%; (2) long, 91–100%.  
Dist.: *Homo* 0; *Pan* 2; *Gorilla* 1; *Pongo* 0; *Hylobates* 0; *Colobus* ?.

80. **Zygomatic bone**  
States: (0) curved; (1) flattened.  
Dist.: *Homo* 0; *Pan* 0; *Gorilla* 0; *Pongo* 1; *Hylobates* 0; *Colobus* ?.

81. **Relative face height**  
States: (0) 19–24; (1) 27–30.  
Dist.: *Homo* 0; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 0; *Colobus* ?.

82. **Canine length as percentage of upper M1 (male)**  
States: (0) short, 61–81%; (1) longer, 101–182%.  
Dist.: *Homo* 0; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 1; *Colobus* ?.

83. **Canine length as percentage of upper M1 (female)**  
States: (0) short, 61–81%; (1) longer, 92–144%.  
Dist.: *Homo* 0; *Pan* 1; *Gorilla* 1; *Pongo* 1; *Hylobates* 1; *Colobus* ?.
84. **Canine length as percentage of upper P4 (male)**
   States: (0) short, 116–160%; (1) longer, 215–543%.
   Dist.: Homo 0; Pan 1; Gorilla 1; Pongo 1; H. sp. 1; Colobus ?.

85. **Canine length as percentage of upper P4 (female)**
   States: (0) short, 116–178%; (1) longer, 187–273%; (2) still longer, 307–543%.
   Dist.: Homo 0; Pan 1; Gorilla 0; Pongo 0; H. sp. 2; Colobus ?.

86. **Angle between tooth rows**
   States: (0) low, 5–16°; (1) high, 20–40°.
   Dist.: Homo 0; Pan 1; Gorilla 0; Pongo 0; H. sp. 0; Colobus 0.

87. **Eruption after upper I2**
   States: (0) PCPM; (1) MPPC.
   Dist.: Homo 0; Pan 1; Gorilla 1; Pongo 1; H. sp. 1; Colobus ?.

88. **Eruption after lower I2**
   States: (0) CPPM; (1) MPPC.
   Dist.: Homo 0; Pan 1; Gorilla 1; Pongo 1; H. sp. 1; Colobus ?.

89. **Upper I1 lingual crenulations**
   States: (0) absent; (1) marginal; (2) whole surface.
   Dist.: Homo 1; Pan 1; Gorilla 1; Pongo 2; H. sp. 1; Colobus ?.

90. **Upper I1 cingulum tubercle**
   States: (0) present; (1) absent.
   Dist.: Homo 0; Pan 1; Gorilla 1; Pongo 0; H. sp. 1; Colobus ?.

91. **Number of upper I1 ridges**
   States: (0) one; (1) one or more than one; (2) always more than one.
   Dist.: Homo 1; Pan 0; Gorilla 2; Pongo 1; H. sp. 0; Colobus ?.

92. **Canine sexual dimorphism**
   States: (0) monomorphic; (1) dimorphic.
   Dist.: Homo 0; Pan 1; Gorilla 1; Pongo 1; H. sp. 0; Colobus ?.

93. **Canine elongation**
   States: (0) buccolingual; (1) none; (2) mesiodistal.
   Dist.: Homo 0; Pan 2; Gorilla 2; Pongo 2; H. sp. 1; Colobus ?.

94. **Lower P3 metaconid**
   States: (0) absent; (1) tiny; (2) small.
   Dist.: Homo 2; Pan 0/1; Gorilla 1; Pongo 2; H. sp. 0; Colobus ?.

95. **Trigonid basin**
   States: (0) narrow slit; (1) fair; (2) wider.
   Dist.: Homo 1; Pan 2; Gorilla 2; Pongo 1; H. sp. 0; Colobus ?.

96. **Sulcus obliquus**
   States: (0) weak to moderate definition; (1) strong to very strong definition.
   Dist.: Homo 0; Pan 0; Gorilla 1; Pongo 1; H. sp. 0; Colobus ?.

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**Appendix 2. Details of the 171 soft-tissue characters used in the study.**

The description of each character is followed by the key to the character states (“States”) and the distribution of character states among the taxa (“Dist”). Further details, including the references for allocating the character states to the taxa, can be found in Gibbs *et al.* (2002).

1. **Omohyoid has three bellies in some specimens**
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 0
2. Anterior bellies of digastric in contact in midline
   States: 0=yes, 1=no
   Dist.:  Hylobates 0, Pongo 0, Gorilla 1, Pan 0, Homo 1

3. Cricothyroid insertion onto external surface of posterior thyroid lamina
   States: 0=yes, 1=no
   Dist.:  Hylobates 0, Pongo 1, Gorilla 1, Pan 0, Homo 1

4. Shape of apex of tongue
   States: 0=rounded, 1=square
   Dist.:  Hylobates 0, Pongo 0, Gorilla 1, Pan 0, Homo 1

5. Presence/absence of apical lingual gland
   States: 0=absent, 1=variable, 2=present
   Dist.:  Hylobates 0, Pongo 0, Gorilla 1, Pan 0, Homo 1

6. Presence/absence of filiform papillae on posterior third of tongue
   States: 0=present, 1=absent
   Dist.:  Hylobates 0, Pongo 1, Gorilla 0, Pan 0, Homo 1

7. Conical filiform predominate over cylindrical filiform
   States: 0=yes, 1=no
   Dist.:  Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 1

8. Sublingual fold is triangular
   States: 0=yes, 1=no
   Dist.:  Hylobates 0, Pongo 1, Gorilla 0, Pan 0, Homo 1

9. Abductor pollicis brevis divides into slips in some specimens
   States: 0=no, 1=yes
   Dist.:  Hylobates 0, Pongo 0, Gorilla 1, Pan 0, Homo 1

10. Occasional reinforcement of abductor pollicis brevis by slips from flexor pollicis brevis
    States: 0=yes, 1=no
    Dist.:  Hylobates 0, Pongo 1, Gorilla 1, Pan 0, Homo 1

11. Abductor pollicis brevis inserts into MI
    States: 0=yes, 1=no
    Dist.:  Hylobates 0, Pongo 1, Gorilla 0, Pan 0, Homo 1

12. Radial head of flexor pollicis brevis originates from flexor retinaculum and trapeziun only
    States: 0=no, 1=yes
    Dist.:  Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 1

13. Site of origin of the humeral head of pronator teres
    States: 0=medial humeral epicondyle, 1=medial humeral epicondyle and medial intermuscular septum
    Dist.:  Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 1

14. Humeroulnar head of flexor digitorum superficialis takes origin from intermuscular septum
    States: 0=no, 1=yes
    Dist.:  Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 1

15. Flexor carpi radialis origin from intermuscular septum
    States: 0=no, 1=yes
    Dist.:  Hylobates 1, Pongo 0, Gorilla 0, Pan 1, Homo 1

16. Flexor carpi radialis fused with flexor digitorum superficialis
    States: 0=no, 1=yes
    Dist.:  Hylobates 0, Pongo 1, Gorilla 1, Pan 1, Homo 0
18. Flexor carpi radialis insertion into palmar surface of base of MIII
States: 0=variable, 1=yes
Dist.: Hylobates ?, Pongo 0, Gorilla 1, Pan 0, Homo 1

19. Palmaris longus present in all specimens
States: 0=no, 1=yes
Dist.: Hylobates 1, Pongo 1, Gorilla 0, Pan 0, Homo 0

20. Flexor carpi ulnaris originates from intermuscular septum
States: 0=no, 1=yes
Dist.: Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 1

21. Flexor carpi ulnaris gives origin to some fibres of flexor digitorum superficialis
States: 0=no, 1=yes
Dist.: Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 0

22. Orientation of pronator quadratus
States: 0=strongly oblique, 1=moderately oblique, 2=weakly oblique
Dist.: Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 2

23. Origin of flexor digitorum profundus extends to medial coronoid process and/or medial humeral condyle
States: 0=no, 1=yes
Dist.: Hylobates 1, Pongo 0, Gorilla 1, Pan 0, Homo 1

24. Flexor pollicis longus originates from anterior radius and interosseous membrane
States: 0=no, 1=yes
Dist.: Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 1

25. Flexor pollicis longus takes origin from palmar fascia
States: 0=no, 1=yes
Dist.: Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 0

26. Flexor pollicis longus gives origin to tendon to digit II
States: 0=no, 1=occasionally, 2=often
Dist.: Hylobates 1, Pongo 0, Gorilla 0, Pan 2, Homo 1

27. Extensor carpi radialis brevis originates from radial collateral ligament
States: 0=no, 1=yes
Dist.: Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 1

28. Extensor carpi radialis brevis originates from intermuscular septum
States: 0=no, 1=yes
Dist.: Hylobates 0, Pongo 1, Gorilla 0, Pan 0, Homo 1

29. Extensor carpi radialis brevis inserts into MII
States: 0=yes, 1=variable, 2=no
Dist.: Hylobates 0, Pongo 2, Gorilla 0, Pan 2, Homo 1

30. Accessory tendon of extensor carpi radialis longus to MI
States: 0=no, 1=sometimes present (~10% specimens), 2=often present (~50% specimens)
Dist.: Hylobates 2, Pongo 0, Gorilla 0, Pan 0, Homo 1

31. Fusion of brachioradialis with brachialis
States: 0=yes, 1=variable, 2=no
Dist.: Hylobates 0, Pongo 2, Gorilla 2, Pan 0, Homo 1

32. Extensor digitorum originates from intermuscular septum
States: 0=no, 1=yes
Dist.: Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 1

33. Extensor digitorum commonly originates from forearm bones
States: 0=radius and ulna, 1=ulna only, 2=neither forearm bone
Dist.: Hylobates 1, Pongo 1, Gorilla 0, Pan 0, Homo 2
34. **Extensor digitorum originates from antebrachial fascia**
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 0, Gorilla 0, Pan 1, Homo 1

35. **Slips from extensor digitorum tendon for digit IV to digits III and V**
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 1

36. **Coracobrachialis origination from intermuscular septum**
   States: 0=no, 1=variable, 2=yes
   Dist.: Hylobates 0, Pongo 0, Gorilla 2, Pan 2, Homo 1

37. **Coracobrachialis fused with brachialis**
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 1, Gorilla 1, Pan 1, Homo 0

38. **Anterior extension of insertion of coracobrachialis present in most specimens**
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 1

39. **Brachialis originates from septa**
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 1, Gorilla 1, Pan 0, Homo 1

40. **Lateral head of triceps brachii originates from lateral intermuscular septum**
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 0, Gorilla 0, Pan 1, Homo 1

41. **Extensor digitorum insertion extends into middle or distal phalanges in some specimens**
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 1, Gorilla 1, Pan 1, Homo 0

42. **Extensor digitorum inserts into interphalangeal joints**
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 0

43. **Extensor digiti minimi absent in some specimens**
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 1

44. **Extension of extensor carpi ulnaris to first phalanx of digit V in some specimens**
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 0, Gorilla 0, Pan 1, Homo 1

45. **Supinator origination from ligaments of elbow**
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 0

46. **Abductor pollicis longus origination from intermuscular septum**
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 0

47. **Extensor pollicis brevis origination from ulna and interosseous membrane**
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 1

48. **Extensor pollicis brevis insertion onto base of proximal phalanx of digit I**
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 0, Gorilla 1, Pan 0, Homo 1

49. **Extensor indicis origination from interosseous membrane**
   States: 0=yes, 1=no
   Dist.: Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 0
50. Most common pattern of insertion of extensor indicis
   States: 0=digits II, III and IV, 1=digits II and III, 2=digit II
   Dist.:  Hylobates 0, Pongo 1, Gorilla 2, Pan 2, Homo 2

51. Deltoid origination from infraspinous fascia
   States: 0=no, 1=yes
   Dist.:  Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 0

52. Teres minor insertion extends onto shaft below greater tubercle
   States: 0=no, 1=yes
   Dist.:  Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 1

53. Teres minor shares origin from intermuscular septum with teres major
   States: 0=no, 1=yes
   Dist.:  Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 1

54. Latissimus dorsi may originate from inferior scapular angle
   States: 0=no, 1=yes
   Dist.:  Hylobates 0, Pongo 0, Gorilla 0, Pan 1, Homo 0

55. Extent of costal origin of latissimus dorsi
   States: 0=three or four ribs, 1=three, four or five ribs, 2=five ribs, 3=six ribs
   Dist.:  Hylobates 2, Pongo 3, Gorilla 3, Pan 1, Homo 0

56. Extent of origin of teres major from lateral scapular border
   States: 0=30%, 1=50%, 2=more than 50%
   Dist.:  Hylobates 2, Pongo 0, Gorilla 0, Pan 1, Homo 0

57. Subscapularis insertion extends onto shaft below lesser humeral tubercle
   States: 0=no, 1=yes
   Dist.:  Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 1

58. Accessory bundles of subscapularis present in some individuals
   States: 0=no, 1=yes
   Dist.:  Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 1

59. Subclavius takes origin on first rib only
   States: 0=no, 1=yes
   Dist.:  Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 1

60. Costal origin of serratus anterior extends to rib 12
    States: 0=no, 1=yes
    Dist.:  Hylobates 0, Pongo 1, Gorilla 1, Pan 1, Homo 0

61. Cranial extent of costal origin of pectoralis major
    States: 0=ribs one and two, 1=rib two only, 2=none
    Dist.:  Hylobates 2, Pongo 0, Gorilla 1, Pan 0, Homo 1

62. Caudal extent of costal origin of pectoralis major
    States: 0=none, 1=rib eight
    Dist.:  Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 0

63. Extent of clavicular origin of pectoralis major
    States: 0=two-thirds, 1=half, 2=third
    Dist.:  Hylobates 0, Pongo 2, Gorilla 2, Pan 1, Homo 1

64. Pectoralis major may divide into three parts
    States: 0=no, 1=yes
    Dist.:  Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 1

65. Origin of psoas major extends to S1
    States: 0=yes, 1=variable, 2=no
    Dist.:  Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 2

66. Coccygeus insertion into anococcygeal raphe
    States: 0=yes, 1=no
    Dist.:  Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 1
67. Coccygeus insertion into sacrum
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 0, Gorilla 1, Pan 0, Homo 1

68. Piriformis normally fused with gluteus medius
   States: 0=yes, 1=no
   Dist.: Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 1

69. Origin of gluteus minimus is continuous
   States: 0=yes, 1=variable, 2=no
   Dist.: Hylobates 0, Pongo 2, Gorilla 2, Pan 2, Homo 1

70. Gluteus medius origination from fascia lata
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 1, Gorilla 1, Pan 1, Homo 0

71. Gluteus medius is bipennate
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 0

72. Tensor fascia latae normally fused proximally with gluteus maximus
   States: 0=yes, 1=no
   Dist.: Hylobates 0, Pongo 0, Gorilla 0, Pan 1, Homo 1

73. Tensor fascia latae fused laterally with gluteus medius and minimus
   States: 0=yes, 1=no
   Dist.: Hylobates 0, Pongo 1, Gorilla 0, Pan 0, Homo 1

74. Gluteus maximus fused with biceps femoris
   States: 0=no fusion, 1=at origin, 2=more distally
   Dist.: Hylobates 1, Pongo 2, Gorilla 1, Pan 1, Homo 0

75. Gluteus maximus insertion into hypotrochanteric fossa
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 1, Gorilla 1, Pan 1, Homo 0

76. Superior gemellus
   States: 0=present, 1=variable, 2=absent
   Dist.: Hylobates 2, Pongo 1, Gorilla 1, Pan 0, Homo 1

77. Quadratus femoris split at insertion
   States: 0=yes, 1=variable, 2=no
   Dist.: Hylobates 0, Pongo 0, Gorilla 2, Pan 1, Homo 2

78. Obturator externus fused at insertion with obturator internus
   States: 0=yes, 1=variable, 2=no
   Dist.: Hylobates 0, Pongo 1, Gorilla 1, Pan 0, Homo 2

79. Gracilis origin extends to whole pubic body
   States: 0=yes, 1=no
   Dist.: Hylobates 0, Pongo 0, Gorilla 0, Pan 0, Homo 1

80. Adductor brevis origination from superior pubic ramus
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 1, Gorilla 1, Pan 1, Homo 0

81. Adductor brevis inserted between pectineus and upper part of adductor magnus
   States: 0=yes, 1=no
   Dist.: Hylobates 0, Pongo 1, Gorilla 1, Pan 1, Homo 0

82. Adductor magnus insertion into inferior border of quadratus femoris insertion
   States: 0=yes, 1=no
   Dist.: Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 1

83. Rectus femoris has two heads
   States: 0=no, 1=variable, 2=yes
   Dist.: Hylobates 0, Pongo 1, Gorilla 1, Pan 1, Homo 2
84. **Vastus medialis origination from intermuscular septa**
States: 0=no, 1=yes
Dist.: *Hylobates* 0, *Pongo* 1, *Gorilla* 0, *Pan* 0, *Homo* 1

85. **Vastus medialis insertion onto medial patellar surface**
States: 0=no, 1=variable, 2=yes
Dist.: *Hylobates* 0, *Pongo* 0, *Gorilla* 1, *Pan* 0, *Homo* 2

86. **Vastus lateralis origination from iliofemoral ligament**
States: 0=no, 1=yes
Dist.: *Hylobates* 0, *Pongo* 1, *Gorilla* 1, *Pan* 1, *Homo* 0

87. **Articularis genus present**
States: 0=yes, 1=variable
Dist.: *Hylobates* 0, *Pongo* 1, *Gorilla* 1, *Pan* 1, *Homo* 1

88. **Origin of short head of biceps femoris**
States: 0=posterolateral femur and lateral intermuscular septum, 1=posterolateral femur only
Dist.: *Hylobates* 0, *Pongo* 1, *Gorilla* 1, *Pan* 0, *Homo* 0

89. **Long head of biceps femoris may insert into iliotibial tract**
States: 0=no, 1=yes
Dist.: *Hylobates* 0, *Pongo* 1, *Gorilla* 0, *Pan* 1, *Homo* 0

90. **Insertion of short head of biceps femoris onto lateral intermuscular septum**
States: 0=no, 1=yes
Dist.: *Hylobates* 0, *Pongo* 1, *Gorilla* 0, *Pan* 1, *Homo* 0

91. **Semitendinosus may share common origin with semimembranosus**
States: 0=no, 1=yes
Dist.: *Hylobates* 0, *Pongo* 1, *Gorilla* 0, *Pan* 1, *Homo* 1

92. **Semimembranosus inserts into popliteal fascia and posterior wall of knee capsule via oblique popliteal ligaments**
States: 0=no, 1=yes
Dist.: *Hylobates* 0, *Pongo* 0, *Gorilla* 1, *Pan* 0, *Homo* 1

93. **Tibialis anterior originates from crural fascia**
States: 0=no, 1=yes
Dist.: *Hylobates* 0, *Pongo* 0, *Gorilla* 0, *Pan* 0, *Homo* 1

94. **Extensor digitorum longus originates from crural fascia**
States: 0=no, 1=yes
Dist.: *Hylobates* 0, *Pongo* 0, *Gorilla* 0, *Pan* 1, *Homo* 1

95. **Incidence of peroneus tertius**
States: 0=low incidence (0–5% of specimens), 1=moderate incidence (30–50% of specimens), 2=high incidence (~95% of specimens)
Dist.: *Hylobates* 1, *Pongo* 0, *Gorilla* 1, *Pan* 0, *Homo* 2

96. **Peroneus longus origination from lateral tibial condyle**
States: 0=yes, 1=no
Dist.: *Hylobates* 0, *Pongo* 1, *Gorilla* 1, *Pan* 0, *Homo* 0

97. **Peroneus brevis may insert onto first and second phalanges of digit V**
States: 0=no, 1=yes
Dist.: *Hylobates* 0, *Pongo* 0, *Gorilla* 1, *Pan* 1, *Homo* 1

98. **Soleus often has tibial origin**
States: 0=no, 1=yes
Dist.: *Hylobates* 0, *Pongo* 0, *Gorilla* 1, *Pan* 1, *Homo* 1

99. **Plantaris often present**
States: 0=no, 1=yes
Dist.: *Hylobates* 0, *Pongo* 0, *Gorilla* 0, *Pan* 1, *Homo* 1
100. Extensor digitorum brevis tendon to digit V normally present
   States: 0=yes, 1=no
   Dist.: Hylobates 0, Pongo 1, Gorilla 1, Pan 0, Homo 0

101. Slip from abductor hallucis into base of MI
   States: 0=yes, 1=no
   Dist.: Hylobates 0, Pongo 0, Gorilla 0, Pan 1, Homo 1

102. Both heads of flexor hallucis brevis fused with abductor hallucis
   States: 0=yes, 1=no
   Dist.: Hylobates 0, Pongo 1, Gorilla 1, Pan 0, Homo 1

103. Two heads of adductor hallucis fused
   States: 0=yes, 1=variable, 2=no
   Dist.: Hylobates 0, Pongo 2, Gorilla 2, Pan 1, Homo 0

104. Oblique head of adductor hallucis origination from sheath of peroneus longus
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 1

105. Abductor hallucis may insert onto medial cuneiform
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 1

106. Medial and lateral heads of flexor hallucis brevis separated by septum
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 1, Gorilla 1, Pan 0, Homo 0

107. Origin of transverse head of adductor hallucis
   States: 0=second and third metatarsophalangeal joints and ligaments, 1=second,
          third and fourth metatarsophalangeal joints and ligaments, 2=third, fourth
          and fifth metatarsophalangeal joints and ligaments
   Dist.: Hylobates 1, Pongo 0, Gorilla 1, Pan 1, Homo 2

108. First dorsal interosseous originates from MI and MII
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 0, Gorilla 0, Pan 1, Homo 1

109. Flexor digitorum brevis originates from plantar aponeurosis
   States: 0=no, 1=yes
   Dist.: Hylobates 0, Pongo 0, Gorilla 0, Pan 1, Homo 1

110. Flexor digitorum brevis may fuse with abductor hallucis
    States: 0=no, 1=yes
    Dist.: Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 0

111. Perforating veins in cubital fossa
    States: 0=present, 1=variable, 2=absent
    Dist.: Hylobates 0, Pongo 2, Gorilla 0, Pan 1, Homo 0

112. Basilic vein
    States: 0=absent, 1=variable, 2=present
    Dist.: Hylobates 0, Pongo 1, Gorilla 1, Pan 0, Homo 2

113. Cephalic vein limited to forearm
    States: 0=no, 1=low incidence (20–25% of specimens), 2=high incidence (80–
          100% of specimens)
    Dist.: Hylobates 0, Pongo 0, Gorilla 2, Pan 2, Homo 1

114. Palmar metacarpal arteries originate from deep palmar arch
    States: 0=yes, 1=no
    Dist.: Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 0

115. Origin of radialis indicus may include first palmar metacarpal artery
    States: 0=no, 1=yes
    Dist.: Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 1
116. **Origin of posterior interosseous artery**
   - **Style:** 0=brachial artery, 1=common interosseous
   - **Dist.:** *Hylabates* 0, *Pongo* 0, *Gorilla* 0, *Pan* 1, *Homo* 1

117. **Dorsalis indicis and dorsal metacarpal branches of ulnar artery**
   - **States:** 0=absent, 1=present
   - **Dist.:** *Hylabates* 0, *Pongo* 1, *Gorilla* 1, *Pan* 0, *Homo* 0

118. **Termination of superficial palmar artery**
   - **States:** 0=thenar muscles, 1=superficial palmar arch
   - **Dist.:** *Hylabates* 0, *Pongo* 1, *Gorilla* 0, *Pan* 1, *Homo* 1

119. **Superficial palmar artery may pass over thenar muscles**
   - **States:** 0=no, 1=yes
   - **Dist.:** *Hylabates* 0, *Pongo* 0, *Gorilla* 0, *Pan* 1, *Homo* 1

120. **Origin of radial recurrent artery**
   - **States:** 0=radial artery, 1=variable, 2=brachial artery
   - **Dist.:** *Hylabates* 0, *Pongo* 2, *Gorilla* 0, *Pan* 1, *Homo* 0

121. **Dorsalis pollicis**
   - **States:** 0=present, 1=absent
   - **Dist.:** *Hylabates* 0, *Pongo* 0, *Gorilla* 0, *Pan* 1, *Homo* 1

122. **Point at which radial artery enters palm**
   - **States:** 0=dorsum of second interosseous space, 1=dorsum of first interosseous space
   - **Dist.:** *Hylabates* 0, *Pongo* 0, *Gorilla* 1, *Pan* 1, *Homo* 1

123. **Superior ulnar collateral artery may originate from brachial artery**
   - **States:** 0=no, 1=yes
   - **Dist.:** *Hylabates* 0, *Pongo* 0, *Gorilla* 1, *Pan* 1, *Homo* 1

124. **Profunda brachii may originate from brachial artery**
   - **States:** 0=no, 1=yes
   - **Dist.:** *Hylabates* 1, *Pongo* 0, *Gorilla* 0, *Pan* 1, *Homo* 1

125. **Lateral thoracic artery normally an independent branch of axillary artery**
   - **States:** 0=no, 1=yes
   - **Dist.:** *Hylabates* 0, *Pongo* 0, *Gorilla* 1, *Pan* 1, *Homo* 1

126. **Pectoral branch of thoracoacromial artery**
   - **States:** 0=absent, 1=variable, 2=present
   - **Dist.:** *Hylabates* 0, *Pongo* 2, *Gorilla* 0, *Pan* 1, *Homo* 2

127. **Superior thoracic artery**
   - **States:** 0=absent, 1=present
   - **Dist.:** *Hylabates* 0, *Pongo* 0, *Gorilla* 1, *Pan* 1, *Homo* 1

128. **Thyroidea ima may arise from left common carotid**
   - **States:** 0=yes, 1=no
   - **Dist.:** *Hylabates* 0, *Pongo* 1, *Gorilla* 0, *Pan* 0, *Homo* 1

129. **Most common form of branches from aortic arch is E (Keith, 1895)**
   - **States:** 0=yes, 1=no
   - **Dist.:** *Hylabates* 1, *Pongo* 0, *Gorilla* 0, *Pan* 0, *Homo* 0

130. **Perforating branch of peroneal artery anastomoses with anterior lateral malleolar artery**
   - **States:** 0=yes, 1=no
   - **Dist.:** *Hylabates* 0, *Pongo* 1, *Gorilla* 0, *Pan* 0, *Homo* 0

131. **Peroneal artery takes origin from posterior tibial artery**
   - **States:** 0=yes, 1=no
   - **Dist.:** *Hylabates* 0, *Pongo* 1, *Gorilla* 0, *Pan* 1, *Homo* 0

132. **Digital branches of deep plantar arch to adjacent sides of digits II and III**
   - **States:** 0=present, 1=variable, 2=absent
   - **Dist.:** *Hylabates* 0, *Pongo* 2, *Gorilla* 0, *Pan* 1, *Homo* 0
<table>
<thead>
<tr>
<th>Number</th>
<th>Description</th>
<th>States</th>
<th>Dist.</th>
</tr>
</thead>
<tbody>
<tr>
<td>133.</td>
<td><strong>Lateral plantar artery dominant</strong></td>
<td>0=no, 1=variable, 2=yes</td>
<td>Hylobates 0, Pongo 0, Gorilla 2, Pan 1, Homo 2</td>
</tr>
<tr>
<td>134.</td>
<td><strong>Inferior medial and inferior lateral genicular branches of popliteal artery</strong></td>
<td>0=present, 1=absent</td>
<td>Hylobates 0, Pongo 1, Gorilla 1, Pan 0, Homo 0</td>
</tr>
<tr>
<td>135.</td>
<td><strong>Medial femoral circumflex artery may originate from profunda femoris</strong></td>
<td>0=no, 1=yes</td>
<td>Hylobates 0, Pongo 0, Gorilla 0, Pan 1, Homo 1</td>
</tr>
<tr>
<td>136.</td>
<td><strong>Three or more perforating branches of profunda femoris</strong></td>
<td>0=no, 1=yes</td>
<td>Hylobates 0, Pongo 0, Gorilla 1, Pan 0, Homo 1</td>
</tr>
<tr>
<td>137.</td>
<td><strong>Muscular branches of profunda femoris for hamstrings</strong></td>
<td>0=no, 1=yes</td>
<td>Hylobates 0, Pongo 0, Gorilla 0, Pan 1, Homo 1</td>
</tr>
<tr>
<td>138.</td>
<td><strong>Muscular branches of profunda femoris for quadriceps</strong></td>
<td>0=no, 1=yes</td>
<td>Hylobates 0, Pongo 0, Gorilla 0, Pan 1, Homo 1</td>
</tr>
<tr>
<td>139.</td>
<td><strong>Number of digits supplied by median nerve</strong></td>
<td>0=normal two and half, 1=normal three and half</td>
<td>Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 1</td>
</tr>
<tr>
<td>140.</td>
<td><strong>Number of digits supplied by radial nerve</strong></td>
<td>0=normal one and half, 1=normal two and half</td>
<td>Hylobates 0, Pongo 0, Gorilla 1, Pan 0, Homo 1</td>
</tr>
<tr>
<td>141.</td>
<td><strong>Gangliform enlargement at junction of radial and posterior interosseous nerves</strong></td>
<td>0=no, 1=yes</td>
<td>Hylobates 0, Pongo 0, Gorilla 0, Pan 1, Homo 1</td>
</tr>
<tr>
<td>142.</td>
<td><strong>Axillary nerve innervates subscapularis</strong></td>
<td>0=no, 1=yes</td>
<td>Hylobates 0, Pongo 1, Gorilla 1, Pan 0, Homo 0</td>
</tr>
<tr>
<td>143.</td>
<td><strong>Origin of axillary nerve</strong></td>
<td>0=C5–7, 1=C5–8, 2=C5–8 and T1</td>
<td>Hylobates 1, Pongo 1, Gorilla 2, Pan 2, Homo 0</td>
</tr>
<tr>
<td>144.</td>
<td><strong>Number of lumbricals innervated by ulnar nerve</strong></td>
<td>0=normal one, 1=normal two, 2=normal three</td>
<td>Hylobates 1, Pongo 1, Gorilla 2, Pan 0, Homo 1</td>
</tr>
<tr>
<td>145.</td>
<td><strong>Ulnar nerve may innervate flexor pollicis brevis</strong></td>
<td>0=no, 1=yes</td>
<td>Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 1</td>
</tr>
<tr>
<td>146.</td>
<td><strong>Ulnar nerve normally supplies hypothenar muscles</strong></td>
<td>0=no, 1=yes</td>
<td>Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 1</td>
</tr>
<tr>
<td>147.</td>
<td><strong>Origin of subscapular nerves</strong></td>
<td>0=C5, C6, 1=C5–7, 2=C5–8, 3=C5–8 and T1</td>
<td>Hylobates 2, Pongo 1, Gorilla 3, Pan 3, Homo 0</td>
</tr>
<tr>
<td>148.</td>
<td><strong>Psoas minor innervated by femoral nerve</strong></td>
<td>0=no, 1=yes</td>
<td>Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 1</td>
</tr>
<tr>
<td>149.</td>
<td><strong>Lateral cutaneous nerve of thigh may originate from L1 and L2</strong></td>
<td>0=no, 1=yes</td>
<td>Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 0</td>
</tr>
</tbody>
</table>
150. Femoral nerve origination
States: 0=L2–4, 1=variable (L2–4 or L1–3), 2=L1–3
Dist.:  Hylobates 0, Pongo 2, Gorilla 0, Pan 1, Homo 0

151. Genitofemoral nerve origination from L2
States: 0=yes, 1=no
Dist.:  Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 0

152. Genitofemoral nerve may pass lateral to psoas major
States: 0=no, 1=yes
Dist.:  Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 0

153. Obturator nerve origination from L1
States: 0=no, 1=yes
Dist.:  Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 0

154. Muscular branches of obturator nerve may include pectineus
States: 0=no, 1=yes
Dist.:  Hylobates 0, Pongo 0, Gorilla 0, Pan 1, Homo 1

155. Muscular branches of medial plantar nerve
States: 0=one medial lumbrical, 1=two medial lumbricals, 2=two medial lumbricals and adductor hallucis
Dist.:  Hylobates 1, Pongo 2, Gorilla 0, Pan 2, Homo 0

156. Number of digital branches of lateral plantar nerve
States: 0=one and a half, 1=two and a half
Dist.:  Hylobates 0, Pongo 1, Gorilla 1, Pan 1, Homo 0

157. Muscular branches of tibial nerve includes flexor digitorum longus
States: 0=no, 1=yes
Dist.:  Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 1

158. Superficial peroneal nerve supplies medial side of digit II
States: 0=yes, 1=no
Dist.:  Hylobates 0, Pongo 0, Gorilla 0, Pan 1, Homo 1

159. Average body hair density
States: 0=high, 1=moderate, 2=low
Dist.:  Hylobates 0, Pongo 0, Gorilla 1, Pan 2, Homo 2

160. Sternal glands
States: 0=present, 1=absent
Dist.:  Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 1

161. Ratio of nipple position to horizontal height index of nipple position
States: 0=2.6, 1=1.7–1.8, 2=1.0–1.1
Dist.:  Hylobates 0, Pongo 2, Gorilla 1, Pan 1, Homo 2

162. Axillary organ
States: 0=absent, 1=present
Dist.:  Hylobates 0, Pongo 0, Gorilla 1, Pan 1, Homo 1

163. Bulbospongiousus origination from ischial ramus
States: 0=yes, 1=no
Dist.:  Hylobates 0, Pongo 1, Gorilla 0, Pan 0, Homo 1

164. Bulbospongiousus origination from perineal body
States: 0=no, 1=variable, 2=yes
Dist.:  Hylobates 0, Pongo 2, Gorilla 1, Pan 0, Homo 2

165. Penile spines normally present
States: 0=yes, 1=no
Dist.:  Hylobates 0, Pongo 1, Gorilla 1, Pan 0, Homo 1

166. Ventral groove in glans penis
States: 0=present, 1=absent
Dist.:  Hylobates 0, Pongo 1, Gorilla 0, Pan 1, Homo 1
167. **Scrotum normally postpenial**  
States: 0=no, 1=yes  
Dist.: *Hylobates* 0, *Pongo* 0, *Gorilla* 0, *Pan* 1, *Homo* 1

168. **Dependency of scrotum**  
States: 0=nondependent, 1=nondependent or semi-dependent, 2=semi-dependent or dependent, 3=dependent  
Dist.: *Hylobates* 1, *Pongo* 0, *Gorilla* 0, *Pan* 2, *Homo* 3

169. **Relative testes size (ratio of observed/predicted body testes size)**  
States: 0=<0.4, 1=>0.4  
Dist.: *Hylobates* 0, *Pongo* 0, *Gorilla* 0, *Pan* 1, *Homo* 1

170. **Urethral papilla**  
States: 0=present, 1=absent  
Dist.: *Hylobates* 0, *Pongo* 1, *Gorilla* 0, *Pan* 1, *Homo* 1

171. **Transverse rugae of vagina**  
States: 0=little developed, 1=well developed  
Dist.: *Hylobates* 0, *Pongo* 0, *Gorilla* 1, *Pan* 1, *Homo* 1

### Appendix 3. Details of the 129 craniodental quantitative characters used in the study

Further details can be found in Collard & Wood (2000).

<table>
<thead>
<tr>
<th>Character</th>
<th>Definition</th>
<th>P25 Breadth between upper second molars (M₂L-M₃L)</th>
<th>P26 Palate depth at incisive fossa</th>
<th>P27 Palate depth at upper second molars</th>
<th>P28 Maxillary alveolar subtense</th>
<th>P29 Upper incisor alveolar length</th>
<th>P30 Upper premolar alveolar length</th>
<th>P31 Upper molar alveolar length</th>
<th>P32 Upper incisor length</th>
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