Morphological affinities of the *Australopithecus afarensis* hand on the basis of manual proportions and relative thumb length

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Abstract

The hands of apes and humans differ considerably with regard to proportions between several bones. Of critical significance is the long thumb relative to other fingers, which is the basis for human-like pad-to-pad precision grip capability, and has been considered by some as evidence of tool-making. The nature and timing of the evolutionary transition from ape-like to human-like manual proportions, however, have remained unclear as a result of the lack of appropriate fossil material. In this article, the manual proportions of *Australopithecus afarensis* from locality AL 333/333w (Hadar, Ethiopia) are investigated by means of bivariate and multivariate morphometric analyses, in order to test the hypothesis that human-like proportions, including an enhanced thumb/hand relationship, originally evolved as an adaptation to stone tool-making. Although some evidence for human-like manual proportions had been previously proposed for this taxon, conclusive evidence was lacking. Our results indicate that *A. afarensis* possessed overall manual proportions, including an increased thumb/hand relationship that, contrary to previous reports, is fully human and would have permitted pad-to-pad human-like precision grip capability. We show that these human-like proportions in *A. afarensis* mainly result from hand shortening, as in modern humans, and that these conclusions are robust enough as to be non-dependent on whether the bones belong to a single individual or not. Since *A. afarensis* predates the appearance of stone tools in the archeological record, the above-mentioned conclusions permit a confident refutation of the null hypothesis that human-like manual proportions are an adaptation to stone tool-making, and thus alternative explanations must be therefore sought. One hypothesis would consider manipulative behaviors (including tool-use and/or non-lithic tool-making) in early hominines exceeding those reported among extant non-human primates. Alternatively, on the basis of the many adaptations to committed bipedalism in *A. afarensis*, we propose the hypothesis that once arboreal behaviors became adaptively insignificant and forelimb-dominated locomotor selection pressures were relaxed with the adoption of terrestrial bipedalism, human-like manual proportions could have merely evolved as a result of the complex manipulation selection pressures already present in extant non-human primates. Both hypotheses are not mutually exclusive, and even other factors such as pleiotropy cannot be currently discarded.
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Keywords: Fossil hominines; Apes; *Australopithecus afarensis*; Hand; Thumb; Manipulation; Manual proportions

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Introduction

Manual proportions, and especially relative thumb length, are among the features most readily distinguishing the hands of humans from those of other Hominidae. Humans display short hands in comparison with those of great apes, with a particularly long thumb in relative terms (Schultz, 1930; Ashley-Montagu, 1931; Midlo, 1934; Jouffroy et al., 1991; Christel, 1993; Watkins et al., 1993; Susman, 1994). These proportions of the human hand are essential for human manipulative skills related with precision grip capability (Napier, 1960; Marzke, 1971, 1997), being essential for bringing together the tips of all the five digits at the axis of the middle finger, and permitting a pad-to-pad (=pulp-to-pulp) contact between the thumb and the remaining digits (Napier, 1960, 1962a,b). On the contrary, these human-like precision grip postures cannot be assumed by the great apes, due to the relative shortness of their thumbs (Napier, 1960), especially compared with the otherwise elongated fingers. (Although tip-to-tip and tip-to-side precision grasping occur in great apes, pad-to-pad precision grip is exclusive of humans, where it is the most frequently used precision grip posture: Christel, 1993.) The long hands of great apes must be rather interpreted as an arboreal adaptation for functioning as a grasping hook during suspension and/or climbing on large-diameter branches (Susman, 1979; Inouye, 1992). Given the fact that the pattern of long hands with a relatively short thumb is shared by orangutans and African apes, which are successive sister taxa for humans, it is more parsimonious to assume—until fossil evidence demonstrates the contrary—that human manual proportions are apomorphic rather than primitive for the hominine clade. The nature and timing of the evolutionary transition from ape-like to human-like manual proportions, however, are still unclear. Deciphering this has been hampered by the lack of well-founded evidence of manual proportions in Plio-Pleistocene hominines, in its turn resulting from the scarcity of associated fossil hand bones. As a result, a secure assessment of the selection pressures originally involved in the emergence of modern human manual proportions has been thus far precluded.

The involvement of tool-related manipulative selection pressures in the evolution of human manual proportions deserves careful consideration and a precise definition of the terms involved. 'Tool-behavior' can be employed to refer simultaneously to both tool-use and tool-making on any type of raw material (Beck, 1980; see also Marzke, 1997, p. 91, footnote 1). 'Tool-use', in turn, can be defined as "the external deployment of an unattached environmental object to alter more efficiently the form, position, or condition of another object", whereas 'tool-making' can be defined as "any modification of an object by the user or conspecific so that the object serves more effectively as a tool" (Beck, 1980, pp. 10 and 11). Tool-use has been documented in a wide spectrum of animal species (Alcock, 1972; Beck, 1980), including primates such as baboons (Beck, 1974), capuchin monkeys (mostly in captivity) (Visalberghi, 1987), and apes both in captivity and in the wild (see review in McGrew, 1993). It seems, however, that important cognitive differences exist with tool-using between monkeys and apes; as a result, imitational learning by observation is prevented in monkeys (Whiten, 1989; Fragaszy and Visalberghi, 1990), which would explain why novel tool-related behaviors in monkeys are not culturally disseminated (Beck, 1974; Visalberghi, 1993). Amongst apes, only chimpanzees show frequent and diverse tool-use in wild environments uninfluenced by humans (McGrew, 1993). This happens in several contexts, including aggression, feeding and hygiene (Goodall, 1963, 1970, 1986; Nishida, 1973; McGrew, 1974, 1992, 1993 and references therein; Teleki, 1974; McGrew et al., 1979; Sugiyama and Koman, 1979; Boesch and Boesch, 1981, 1984, 1990; Nishida and Hiraiwa, 1982; Kortlandt, 1986), even associated with cultural variation (Sabater Pi, 1984; McGrew, 1992; Whiten et al., 1999). Chimpanzee tool-behavior not only involves tool-use of natural objects, but also in many instances modification of them (e.g. Teleki, 1974; Boesch and Boesch, 1990), i.e. tool-making. In the wild, however, chimpanzee tool-making behavior is limited to organic raw materials, whereas tool making with lithic raw materials (hereafter termed stone tool-making) has only been documented for humans. Moreover,

unlike humans, chimpanzees manufacture all their tools with their teeth and hands, and do not use secondary tools (i.e. tools to make tools), at least in the wild (McGrew, 1993). From the viewpoint of comparative ethology, the last common ancestor of African apes and humans might have been either an accomplished tool-user like chimpanzees, a non-tool-user like gorillas, or something intermediate (McGrew, 1989, 1993). As pointed out by Susman (1995, p. 589), "we might suspect (although there is no evidence of either tools or anatomy) that the earliest hominids used tools in an apelike fashion", and it has even been suggested that they engaged in tool-behaviors more sophisticated than those practiced by extant apes (Marzke, 1997). As stressed by Susman (1995), however, "without tools and without any anatomical traces, we can only speculate about tool-behavior at this early point in the human career". The recent finding that chimpanzee tool-using behavior can leave evidence in the archeological record (Mercader et al., 2002) is very promising for the future discovery of such tool-using activities, but since only lithic industries have been thus far documented, we are restricted to stone tool-making as the hypothesis to be tested (see subsequently).

The morphological features that permit human-like precision grasping have been equated with tool-behavior and "the enhanced ability to manipulate tools" by Susman (1998, p. 24, and 1994, p. 1570, respectively). However, as noted by Marzke (1997, p. 91, footnote 1), in some instances the term tool-behavior has been employed to refer to tool-using and/or non-human tool-making, whereas in other instances (Susman, 1991) it has been employed to refer exclusively to human tool-making. Susman attributes the equation between human-like precision grasping features and tool-making to Napier (e.g. Susman, 1988, p. 169, 1994, p. 1572, 1998, p. 23), considering them as a 'tool-making criterion' (Susman, 1994, p. 1572). However, if human-like precision grasping features are diagnostic of tool-making, as Susman argues, then it follows that these features, including human-like manual proportions, must have originally evolved as an adaptation for tool-making. Although this is conceivable, current function must not be

necessarily equated with evolutionary origin (Gould and Vrba, 1982), so alternative hypotheses are also possible. In this article, we test the hypothesis that the selection of human-like manual proportions, including an enhanced thumb/hand relationship approximating a human-like precision grasping, was originally linked with manipulative selection pressures driven by *stone* tool-making selection pressures. To do so, we rely on the manual remains of *Australopithecus afarensis*, computing its manual proportions and comparing them with those of extant apes and humans by means of univariate and multivariate morphometric techniques. Unlike later australopith species (both *Australopithecus* spp. and *Paranthropus* spp.), *A. afarensis* precedes by about 1 Myr or so the appearance of stone tools and cut-marks in the archeological record at ca. 2.5 Ma of age (Semaw et al., 1997; de Heinzelin et al., 1999), thus providing a meaningful test for the mentioned hypothesis. In order to be able to accept hypotheses of adaptation in the fossil record, "it is minimally necessary … that historical concordance be true for the characters under consideration" (Lauder, 1991, p. 15; see also Greene, 1986). Therefore, our null hypothesis would be rejected if it could be demonstrated that *A. afarensis* already possessed human-like manual proportions, thus considerably predating the appearance of stone tool-making in the record. As we have already mentioned, other tool-related behaviors (tool-using and non-lithic tool-making) cannot be incorporated into the null hypothesis because it is not currently possible to discern between real and artifactual absence of traces of these behaviors in the record. Of course, many other qualitative and quantitative morphological characters, including robusticity and morphology of articular surfaces, are important in relation to human manipulative skills, but their investigation is outside the scope of this paper and will be discussed in detail elsewhere (Moyà-Solà et al., in preparation; Alba et al., in preparation).

The issue raised in this paper has remained unresolved until now because of the controversy surrounding the morphological affinities of the hands of early hominines. The most complete specimen was until recently O.H. 7 from Olduvai Gorge (Napier, 1962b; Leakey et al., 1964; Susman

and Creel, 1979), which lacks the first metacarpal and proximal phalanx, and in general is too incomplete to provide a meaningful comparison of manual or thumb proportions. Accordingly, previous assertions on this subject have been restricted to *A. afarensis* from Hadar. In spite of the abundant manual remains of this species from locality AL 333/333w (Bush, 1980; Bush et al., 1982), two different views can be found in the literature with regard to the morphological affinities of the *A. afarensis* hand. According to Stern and Susman (1983), the hand of *A. afarensis* would be essentially ape-like, i.e. "a suspensory adapted hand, surprisingly similar to hands found in the small end of the pygmy chimpanzee–common chimpanzee range" (Stern and Susman, 1983, p. 284). For Susman, this would be true not only in a locomotor context, but also in a manipulative one, asserting that "*A. afarensis* has a chimpanzee-like thumb" (Susman, 1995, p. 589) on the basis of thumb robusticity (metacarpal I head breadth/length). On the contrary, according to Marzke (1983, 1986, 1997), the hand of *A. afarensis* would already display some human-like characters (i.e. features more similar to modern humans than to living apes). Proportions between several hand bones have not played a very prominent role in this discussion, however, probably due to the problems associated with their quantification, since more than one single bone is required. For example, Stern and Susman's (1983) account of the *A. afarensis* hand as essentially ape-like made no explicit mention of manual proportions. Later on, Susman (1994) relied on thumb robusticity as a 'toolmaking criterion' (p. 1571) additional to the "morphological criteria for toolmaking proposed by Napier in the early 1960s, including, among others, a fully opposable thumb with increased relative thumb length…" (p. 1572). And he did so in spite of recognizing that "The length of the thumb relative to the fingers is the most appropriate comparison" (Susman, 1995, p. 589), because the latter criterion is "limited to individual hominid specimens that are represented by associated hand bones (necessary to calculate thumb and finger proportions)" (Susman, 1994, p. 1572). Marzke (1983; see also 1997), who nevertheless investigated this issue, concluded that the thumb

of *A. afarensis* "was longer in proportion to the fingers than in pongids" (1983, p. 197). This confirmed the earlier report of Bush (1980, p. 210), according to which relative thumb length in this taxon would be "relatively short compared to *H. sapiens* but relatively long compared to modern pongids". The latter two authors therefore suggested derived thumb/hand proportions for *A. afarensis*, but still intermediate between extant apes and modern humans. This is shown by the fact that Marzke (1997, p. 105) considers that in *A. afarensis*, "The thumb probably was not long enough to facilitate pad-to-pad precision pinch and handling of small tools by the thumb and distal finger pads". In any case, these somewhat human-like proportions in the hand of *A. afarensis* would at least partially result from finger shortening, as shown by Latimer (1991). The latter concluded, on the basis of third proximal phalanx relative length, that the finger bones in Hadar hominids "are shorter than any other hominoid (except *Homo*) indicating that they had undergone directional selection for length reduction" (Latimer, 1991, p. 169). Trinkaus (1992, p. 347), finally, also concluded that the hands of *A. afarensis* and other australopiths "lack either thumb foreshortening or elongation of the other fingers", with "relative finger lengths … similar to those of modern humans", although he did not provide any indication on what analyses his commentaries were based.

With regard to manual proportions, all the above-mentioned analyses must remain tentative because the manual elements from locality AL 333/333w include a mixed array of isolated bones from several individuals. Consequently, it would be possible to argue that the reported, somewhat human-like proportions are merely artifactual, i.e. that they result from computing proportions from bones belonging to different individuals. After a close examination of good-quality casts of hand bones from locality AL 333/333w, we have come to the conclusion that many of these bones probably belong to the same individual (see discussion in Section 2), but since the bones were not found in anatomical connection, doubts remain. Susman (1998), in particular, has recently criticized the use of relative thumb length in *A. afarensis* on the

basis that the lack of a firm association between the recovered hand bones makes this measurement unreliable. A rigorous quantitative assessment of manual proportions in this taxon, taking this caveat into account, is therefore required. In fact, Watkins et al. (1996) already concluded that the bones of digital rays I–IV (but not V) of the *A. afarensis* composite hand set could be modeled as belonging to a single individual, but unfortunately no further details have been provided since their initial preliminary report. In this paper, we show by means of randomization analyses that firm conclusions can be reached on the manual proportions of this taxon *even if the bones do not belong to the same individual*. This is very promising, since until more evidence is available for more ancient species such as *Ardipithecus* (White et al., 1994) and *Orrorin* (Senut et al., 2001), or from the nearly complete hand (and skeleton) of *A. africanus* from Sterkfontein (Clarke, 1999), *A. afarensis* remains central for understanding the origin of human-like manual proportions. We will demonstrate that this confirms the previous assessment of Watkins et al. (1993, 1996), according to which, in comparison to body mass, the thumb of *A. afarensis* would be nearly as elongated as in modern humans (in comparison to African apes), whereas the length of the remaining manual rays would be reduced to the same degree. Moreover, we further refine and extend these conclusions, by showing that: (1) besides relative thumb length, *A. afarensis* has overall human-like manual proportions (an aspect previously not directly addressed by other authors), which contradicts the previous interpretation of it having an essentially ape-like, suspensory-adapted hand (e.g. Stern and Susman, 1983); (2) the increased thumb/hand relationship of *A. afarensis* is not only derived towards the human condition (thus confirming Bush, 1980 and Marzke, 1983), but also that, as in living humans, this mainly results from hand shortening (as first shown by Latimer, 1991) and only to a lesser extent (if at all) from thumb lengthening (thus confirming Watkins et al., 1993, 1996); (3) the relative length of the *A. afarensis* thumb is not intermediate between modern humans and apes (as previously asserted by Bush, 1980 and Marzke, 1983), but almost fully human, being thus probably capable of making pad-to-pad precision grasping (contra Marzke, 1997); and (4) these conclusions are valid even if the bones do not belong to a single individual. This allows us to confidently refute the null hypothesis that human-like manual proportions originally evolved as an adaptation to stone tool-making selection pressures. Several possible alternative hypotheses, taking into account both manipulative and locomotor selection pressures, are therefore discussed.

Material and methods

The fossil sample

A reconstruction of the *A. afarensis* hand when compared with that of living great apes and humans, based on the assumption that many of the manual remains from locality AL 333/333w belong to the same individual, has been provided in Fig. 1. This reconstruction includes the following bones: AL 333w-39, AL 333w-48, AL 333w-16, AL 333-56 and AL 333w-89 (metacarpals I–V); AL 333-69, AL 333-93, AL 333-63, AL 333x-19 and AL 333-62 (proximal phalanges I–V) and AL 333-7, AL 333-88 and AL 333-64 (middle phalanges II, III and V). When bones from left and right hand are combined, the reconstruction only lacks the fourth middle phalanx, which was therefore not included in the comparative analysis. Measurements for *A. afarensis* bones were taken from the literature (Bush et al., 1982). The assignment of the hand bones to a particular manual ray was attempted on the basis of existing criteria (Ricklan, 1988), and the assumption that they could belong to the same individual was made on the basis of size-compatibility and the great congruence found between articular facets. This assumption cannot be unequivocally demonstrated on taphonomical grounds, because at least three large-bodied and two small-bodied adult individuals are represented at this site (McHenry, 1992), and most of the fossils were not found in situ in anatomical connection, but scattered over an area of a few square meters (Johanson et al., 1982). However, this assumption is well substantiated on detailed morphological comparisons (Moyà-Solà
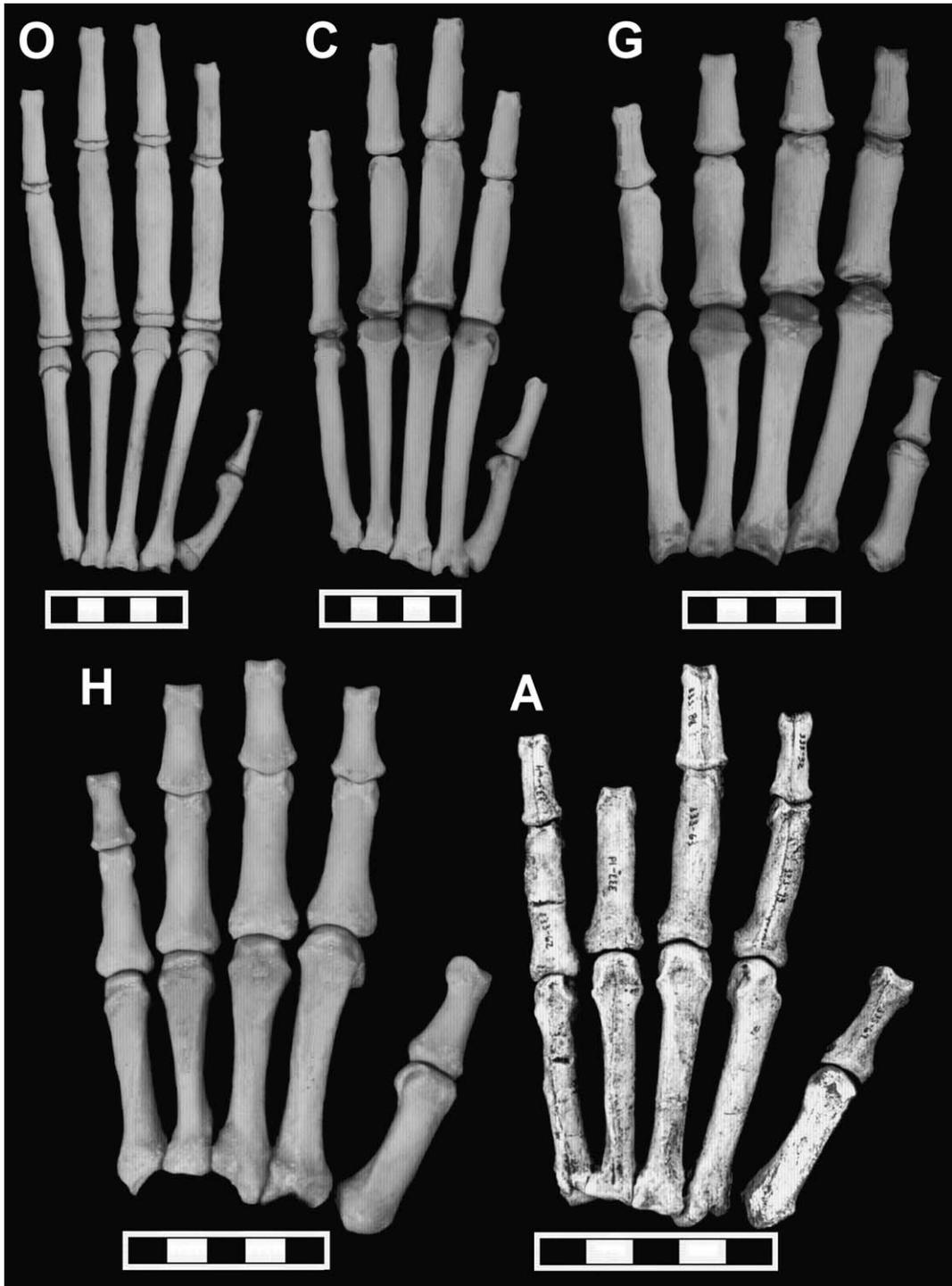
Fig. 1. Composite photograph of our reconstruction of the *A. afarensis* (A) hand from Hadar (locality AL 333/333w), employing left and some right (specular images) bones, when compared with the hands of *P. pygmaeus* (O), *G. gorilla* (G), *P. troglodytes* (C) and *H. sapiens* (H), all scaled to the same size in order to show proportional differences. Scale bar=5 cm.

Table 1

Body mass estimates for *A. afarensis* postcranial specimens from locality AL 333/333w/333x (after McHenry, 1992: Table 4)

Regression	*N*	Mean	± 20%		95% CI		Range	
Hominoid	13	56.2	44.9	67.4	45.1	67.3	34.4	91.2
Human	13	46.1	36.9	55.3	37.6	54.6	21.8	70.2
Average	13	51.1	40.9	61.4	41.8	60.5	28.3	80.7

Specimens included: AL 333-107, AL 333x-14, AL 333-106, AL 333-3, AL 333w-40, AL 333-4, AL 333w-56, AL 333x-26, AL 333-42, AL 333-6, AL 333-7 and AL 333-96; AL 333-95 was excluded because of its subadult status.

Abbreviations: *N*, sample size; CI, confidence interval.

et al., in preparation) and, indeed, we will show that our conclusions are robust enough as to be supported even if the fossils had been collected at random from an *A. afarensis* mixed sample of many individuals.

Body mass estimates

Body mass estimates for specimens from locality AL 333 (Table 1, after McHenry, 1992) were taken from the literature. A total of 13 estimates for adult postcranial remains were considered. Although estimates based on both hominoid and human regressions were taken into account, the average of human estimates was preferred. However, in order to reflect uncertainty in body mass prediction, the 95% confidence interval for the mean, as well as the ± 20% range around the mean (cf. Delson et al., 2000) and the maximum–minimum range have been reported. According to Delson et al. (2000, p. 31), "the range of mean estimates can provide a first approach to an estimation range, while a closer estimate might be obtained from the 20% range around the grand mean". In order to be conservative, we defined the uncertainty range of body mass estimates in *A. afarensis* from locality AL 333 as the maximum and minimum range by taking hominoid and human estimates simultaneously.

The comparative sample

With regard to the comparative sample of extant primates, measurements from a total of 332 hands of adult great apes (237 of known sex, and 80 with associated body mass records) were employed, including specimens of the five extant species: pygmy chimpanzees or bonobos (*Pan paniscus*, *N*=29), common chimpanzees (*Pan troglodytes*, *N*=76), gorillas (*Gorilla gorilla*, *N*= 98), orangutans (*Pongo pygmaeus*, *N*=48), and humans (*Homo sapiens*, *N*=81). Also, some unsexed specimens of white-handed gibbon (*Hylobates lar*, *N*=6), not included in the analysis, were measured to serve as a comparison in allometric plots. The sample consisted of adult specimens, as determined by eruption of the third molar and/or phalangeal epiphyseal fusion. Many of the measured hands were articulated or adequately labeled, so ray attribution was usually not problematic; in the remaining cases, additional criteria were employed (in complete hands, length alone would suffice in most cases with the exception of orangutans; see Susman, 1979), and specimens were rejected when doubts remained. Most of the specimens were measured by one of the authors (D.M.A.) or kindly provided by E. Sarmiento (180 of the 332 measured specimens). Interobserver error was investigated in 16 bonobos that were measured both by D.M.A. and by Sarmiento (a total of 184 available measurements for comparison): mean absolute error (measurement-Alba − measurement-Sarmiento) was found to be 0.33 (95% CI 0.26–0.40, range 0.00–4.05), whereas mean relative error (absolute error/measurement-Alba × 100) was found to be 0.70% (95% CI 0.55–0.85%, range 0.00–8.86%). Thus, with a few exceptions mean relative error was under 1%, so that interobserver differences can be considered negligible.

Measurements and statistical analyses

In order to investigate manual proportions, we measured the maximum length of metacarpals and phalanges (proximal and middle), and also employed the length of the third manual ray as a measure of hand length, and the length of the first manual ray as measure of thumb length. Indices of thumb length in relation to the third manual ray have been employed since Schultz (1930). There is, however, a controversy on the type of relative size measurements that should be used in morphometrics; in particular, a generalized agreement has not been reached yet on the use of ratios vs. residuals (e.g. Corruccini, 1987). Many empirical studies have shown that allometry (i.e. "the change in shape with size": Corruccini, 1987, p. 290) is much more frequent than isometry or geometric similarity (i.e. the lack of correlation between size and shape). As indicated by Corruccini (1987, pp. 291–292): "If allometry is an ubiquitous natural phenomenon, residual size effects will automatically remain in data transformed by linear methods to remove or cancel size"; unfortunately, any "further attempt to correct or remove allometric effects in shape variables seems particularly controversial". Jungers et al. (1995), for example, have criticized the use of residuals as morphometric variables, arguing that "the statistical requirement of independence between size and shape … has no biological justification" (Jungers et al., 1995, p. 153), and concluding that the use of residuals is not recommended when the aim of the study "is to identify individuals … of the same shape after accounting for overall size differences" (Jungers et al., 1995, p. 137).

On the other hand, authors such as Albretch et al. (1993, 1995) have criticized simple ratios and favored the use of residuals, because the former only control for size differences "under special conditions rarely encountered in morphometrics" (Albretch et al., 1993, p. 463). As a result, ratios generally fail to remove size-scaling effects, and are thus potentially misleading when functional inferences are involved, not only in morphological, but also in physiological investigations (Packard and Boardman, 1999). Whereas simple ratios "control isometric size effects but not allometric aspects of

shape correlated with size", regression residuals have the advantage that "measure only those portions of shape uncorrelated with size" (Albretch et al., 1995, p. 195), and "remove size influences without altering distributional characteristics of the original measurement value" (Albretch et al., 1993, p. 465). The only disadvantage is that allometric residuals are no longer an inherent property of the individual (shape), but a relative measurement that depends on the group selected for comparison. Although both ratios and residuals are measures of relative size (proportions), only the former can be truly considered shape measurements.

In the present study on manual proportions, we employed logarithmic residuals in order to ensure that the similarities and/or dissemblances found between *A. afarensis* and extant hominoid species do not artifactually result from scaling effects. These residuals were computed relative to both third manual ray length (to reflect intrinsic manual proportions) and body mass (to reflect the relative elongation of the hand in comparison with the rest of the body). Given the above-mentioned controversy, however, we also checked these results by means of both shape ratios (indices) and raw measurements. Allometric residuals are "the deviations of actual measurements from the value expected for an 'average' specimen of that particular size" (Klingenberg, 1998, p. 35). They were computed by fitting the allometric equation ($\log y = b \log x + a$) to logarithmically transformed data (natural logarithms) by means of linear regression (least-squares), and employing it as a criterion of subtraction (e.g. Gould, 1975). Adult interspecific allometric regressions were based on mean specific data (sexes separated), in order to test for "biomechanical scaling", in which "interspecific proportion differences are required in order to maintain functional equivalence at different body sizes" (Shea, 1983, p. 35). When taxa fall close to the best-fit line, then it is inferred that they do not show any particular adaptation to this regard, so that shape differences are merely attributable to size. On the contrary, when one particular taxon considerably departs from the regression line, specific selection for altered proportions is inferred (Shea, 1983). Extant great apes

and humans were selected as the comparative group, but humans were excluded from the regressions involving the first manual ray, because they were clear outliers and would have rendered the regressions meaningless. Regressions with body mass data were performed with the small available sample of individuals with recorded body mass, but an alternative approach (not reported) showed that the same conclusions would be reached by using the complete database and average body masses taken from the literature.

The several measurements of length (absolute lengths, shape ratios and residuals of relative length) for first and third manual rays were compared, in the case of *A. afarensis* by means of the 95% confidence intervals for the mean, and between living humans and great apes by means of an analysis of variance (ANOVA) and post-hoc multiple comparisons (Bonferroni's method). Although males and females were treated as separate points for deriving allometric equations, for the rest of the analysis they were considered together in a mixed sample, since the sex of the *A. afarensis* fossils is unknown. The overall affinities in manual proportions between *A. afarensis* and other taxa were investigated by means of multivariate canonical (discriminant) analysis. Both absolute lengths and shape ratios, as well as allometric residuals of relative length (both in relation to third manual ray length and body mass), computed for metacarpals, proximal phalanges and middle phalanges, were employed (13 instead of 14 variables were employed, since middle phalanx IV was not available for *A. afarensis*). The effectiveness of these analyses was measured by the percentage of correctly classified original cases by employing cross-validation (leaving out from the analysis the individual being classified). *A. afarensis* was not initially included in the canonical analysis because the aim of the study was precisely to determine its greatest similarities among extant taxa, and including a single fossil specimen (that moreover could belong to more than one individual) could distort the relationships between extant taxa. As noted by Oxnard (1972), this might be a problem if affinities were determined on the basis of canonical variates alone, instead of Mahalanobis

square distances (D^2). For this reason, although we visually depicted the similarities of *A. afarensis* with extant taxa by means of bivariate plots of second vs. first canonical axes, its greatest similarities were determined on the basis of Mahalanobis square distances and further depicted by means of UPGMA (Unweighted Pair Group Method with Arithmetic Mean) cluster diagrams performed with the Mahalanobis square distances between group centroids and the *A. afarensis* scores. All the computations, graphics and statistical analyses were performed with Excel 2000 and SPSS v. 10.

The randomization approach

To test the robustness of our results, i.e. in order to exclude that our results could be due to mixing bones belonging to several *A. afarensis* specimens with ape-like manual proportions, we followed a randomization approach. In particular, we generated at random chimeric hands composed of bones from many individuals, which were later used to replicate the multivariate and bivariate comparisons of *A. afarensis* with extant hominoids. Our approach can be therefore considered conservative, in the sense that we assumed the most extreme condition, i.e. all or at least most of the bones of the *A. afarensis* composite hand coming from different individuals. Thus, for each of the five hominoid species being compared (chimpanzees, bonobos, gorillas, orangutans and humans), we randomly generated a sample of 1000 chimeric hands (each being composed of bones of different individuals from the same species, selected at random). These chimeric hands were generated in the following way: given a certain species and variable, a computer-generated random number was assigned to each measurement (including BM), and this number was then employed to randomly arrange the measurements; this procedure was repeated until 1000 randomly ordered measurements existed for the variable at issue; then, this procedure was repeated for each variable and species; and finally, the randomly ordered measurements for all the variables of the same species were combined in order to generate the sample of 1000 bonobo, chimpanzee, gorilla,

orangutan and human chimeric hands. These were then employed to test the robustness of both bivariate and multivariate (discriminant) analyses by employing both shape ratios and residuals (including BM residuals). In the case of bivariate comparisons, only bones from the first and third manual rays of the chimeric hands were employed, whereas in the case of multivariate comparisons, all the bones except middle phalanx IV (absent in the *A. afarensis* composite hand) were considered.

Essentially, the randomization approach served to estimate the probability of artifactually finding certain manual proportions by mixing bones from several individuals. Both for multivariate and bivariate analyses, two steps were followed: first, we computed the probability of a chimeric hand from a given extant species; being assigned to another (or the same) extant species and second, we computed the probability of a chimeric hand of a given extant species being as similar as *A. afarensis* is to its most similar extant species. In the case of multivariate analyses, chimeric hands were classified by means of the same canonical functions employed to classify the *A. afarensis* composite hand, on the basis of raw data, ratios and several types of residuals. The probability of a chimeric hand being classified as a given extant species was estimated as the proportion of chimeric hands classified in this way by the discriminant analysis. The probability of a chimeric hand being as similar as *A. afarensis* is to its most similar extant species was then estimated as the percentage of chimeric hands showing a Mahalanobis distance equal or smaller than *A. afarensis* to the centroid of its most similar extant species. In the case of bivariate comparisons, the probability of a chimeric hand being classified as a given extant species was estimated as the percentage of chimeric hands falling within the 95% interval for the mean of this extant species. Then, the probability of a chimeric hand being as similar as *A. afarensis* is to its most similar extant species was estimated as the proportion of chimeric hands showing a difference between raw data measurements, ratios or residuals (depending on the case) equal or lower than *A. afarensis* to the mean of its most similar extant species. The above-mentioned probabilities were taken to indi-

cate the chance of misidentifying the true morphological affinities of *A. afarensis* if our assumption that the bones employed belong to the same individual was violated. The standard significance level of 0.05 was required in order to reject the null hypothesis that the manual proportions of *A. afarensis* could result simply from mixing bones from several individuals. Note that the methodology employed in this randomization approach represents the most extreme possibility for the hand bones included in our reconstruction (i.e. all or most the bones coming from different individuals), and is therefore conservative in the sense that tends to maximize the probability of misidentifying the true morphological affinities of a particular hand.

Results

Overall manual proportions

The results of multivariate canonical (discriminant) analyses have been reported in Figs. 2 and 3 and Tables 2–5 (see also the allometric regression equations derived to compute the logarithmic residuals in Table 6). All the different types of variables employed performed approximately equally well for discriminating among living species (Table 5), with more than 90% of correctly classified cases in all instances, and most of the misclassifications produced between bonobos and chimpanzees (not surprisingly, since they belong to the same genus). The results obtained were very similar irrespective of the type of variable employed. On the basis of first and second canonical axes (Fig. 2), chimpanzee and bonobo centroids fell very close to one another, and humans were approximately equidistant from them and from orangutans, and closer to gorillas. With regard to the first canonical axis, which explains most of the variance, African apes were found to be indistinguishable from one another, but clearly distinct from both orangutans, on the one hand, and humans, on the other. With regard to the second axis, which still explains a considerable amount of variation, a gradient was
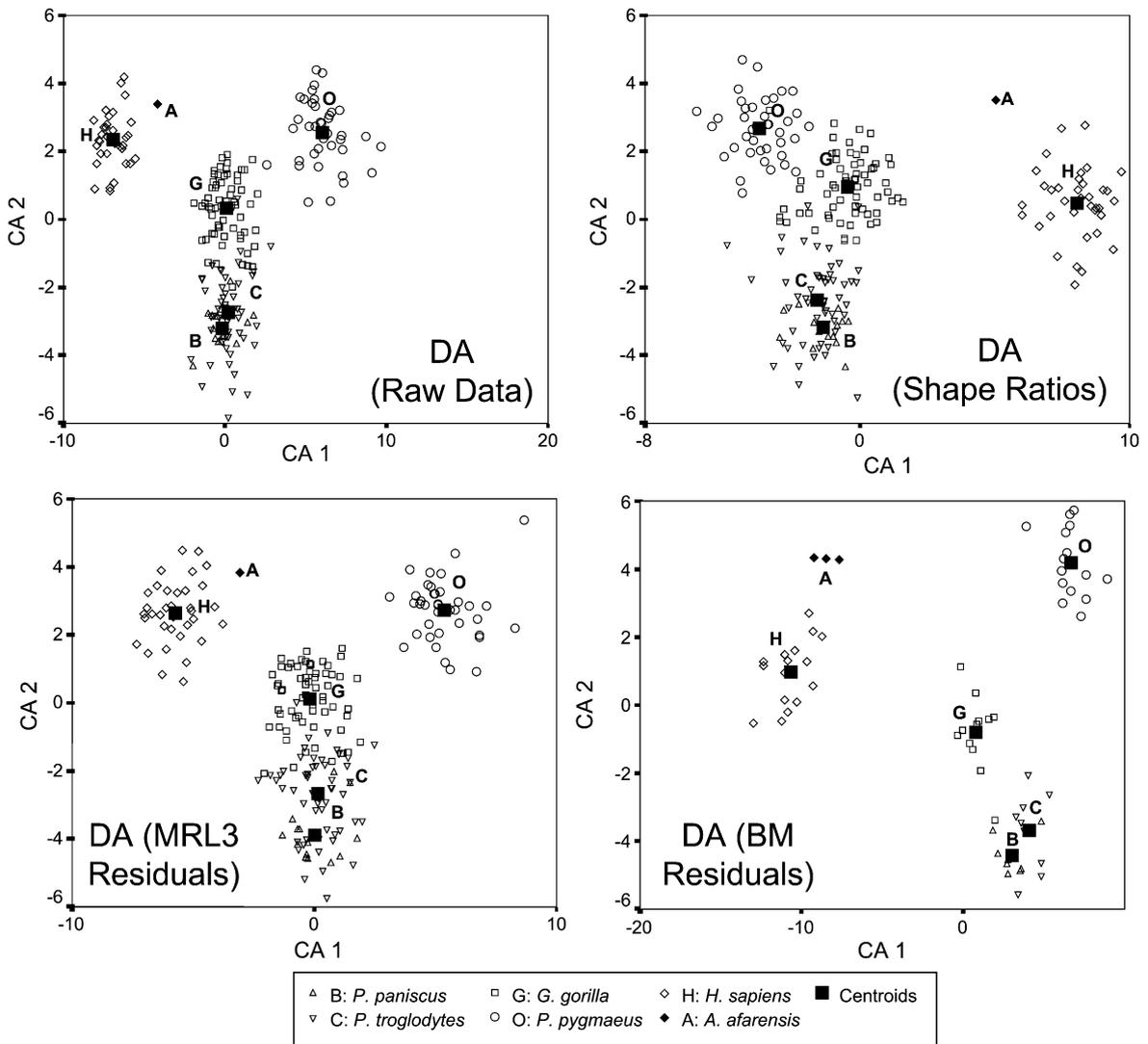
Fig. 2. Data points and group centroids on a plot of second vs. first canonical axes by using raw data, shape ratios and logarithmic residuals (both relative to third manual ray length and body mass). The variance explained by these axes is, respectively: 91% (CA1 68% and CA2 22%); 92% (CA1 73% and CA2 19%), 87% (CA1 58% and CA2 30%) and 97% (CA1 80% and CA2 17%).

found from bonobos to orangutans (bonobos, chimpanzees, gorillas and orangutans, with humans intermediate between the latter two in most instances), thus permitting discrimination between different African ape species. When all canonical axes were considered in a cluster diagram (Fig. 3), bonobos always were found to be most similar to chimpanzees, and they together were more similar to gorillas; the only significant

difference found when using different types of variables was that African apes as a whole sometimes clustered with humans, and in other instances with orangutans.

With regard to *A. afarensis*, in all instances it fell closer to the human centroid (albeit outside the human scatter of points) (Fig. 2) and clustered with humans (Fig. 3), showing a difference comparable to that found between different genera of
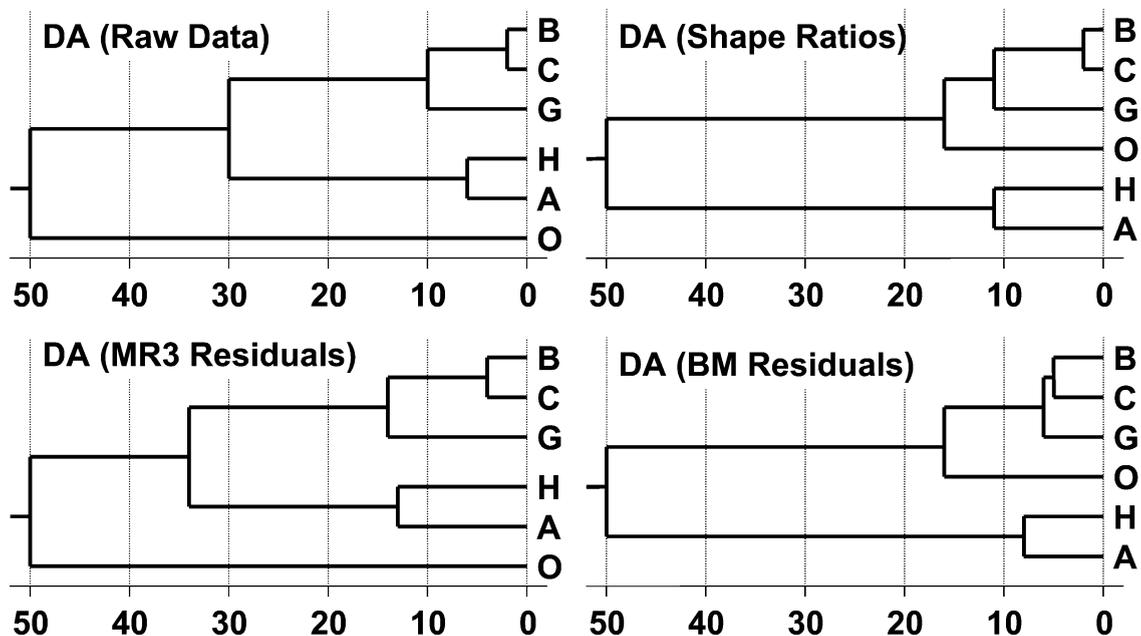
Fig. 3. UPGMA cluster diagrams based on Mahalanobis square distances between group centroids and the position occupied by *A. afarensis*. Abbreviations: B, *P. paniscus*; C, *P. troglodytes*; G, *G. gorilla*; O, *P. pygmaeus*; H, *H. sapiens*; A, *A. afarensis*.

African apes (*Pan* and *Gorilla*). Accordingly, all the different analyses classified in first instance *A. afarensis* as a human (Table 5), although with a probability that indicates significant differences at the 0.05 level (with raw data) or even 0.001 level (ratios and residuals). In the case of BM residuals, this is true even when the maximum and minimum BM estimates for locality AL 333 are employed. In all cases, the *A. afarensis* composite hand was classified in second instance as a gorilla, but with notoriously higher Mahalabonis square distances. This is understandable, given the fact that gorillas were found to be closer (i.e. more similar) to humans than either to chimpanzees or orangutans. This evidence together indicates that, although *A. afarensis* can be excluded from the variability of modern humans, it displays human-like instead of ape-like manual proportions. In all analyses, *A. afarensis* somewhat differed from humans by being somewhat more similar to apes on the first axis, and more similar to orangutans (not to African apes) on the second. This is consistent with *A. afarensis* manual proportions being already derived in the

human direction, but not to such an extent as in living humans.

The results of the randomization analysis undertaken with chimeric hands for the multivariate comparisons have been reported in Table 7. They show that the probability of finding human proportions for a human chimeric hand is very high (>0.95), whereas the probability of misclassifying it as an ape-like hand can be dismissed on statistical grounds (<0.05). Similarly, the possibility of classifying as human-like the chimeric hand of a great ape species can be rejected on statistical grounds in most instances, with the exception of gorillas (all types of variables) and chimpanzees (BM residuals only). Even in the latter cases, the probability of misclassification is very low (0.06–0.11), and in fact, this possibility can also be dismissed when the degree of similarity between humans and the *A. afarensis* composite hand is taken into account. This can be seen in the last column of Table 7, which reports the probability of finding a great ape chimeric hand as similar to human hands as the *A. afarensis* composite hand is. This possibility can be rejected on statistical

Table 2
Results of canonical discriminant analyses with raw data, shape ratios and logarithmic residuals (both relative to third manual ray length and body mass), including group centroids and discriminant scores for *A. afarensis* (in the case of BM residuals, average BM estimation on the basis of human regressions, as well as minimum and maximum BM estimates have been included; see Table 1)

	Raw data				Shape ratios			
	CA1	CA2	CA3	CA4	CA1	CA2	CA3	CA4
Eigenvalue	15.35	5.03	1.82	0.23	14.91	3.98	1.42	0.18
% Variance	68.44	22.43	8.10	1.03	72.77	19.44	6.94	0.86
Canonical correlation	0.97	0.91	0.80	0.43	0.97	0.89	0.77	0.39
P. paniscus	−0.18	−3.21	−1.29	−1.41	−1.40	−3.17	0.96	1.22
P. troglodytes	0.19	−2.73	−0.53	0.51	−1.61	−2.38	0.14	−0.45
G. gorilla	0.09	0.32	1.98	−0.10	−0.50	0.95	−1.65	0.12
P. pygmaeus	6.05	2.55	−1.08	0.01	−3.74	2.67	1.48	−0.03
H. sapiens	−6.95	2.34	−0.98	0.04	8.03	0.48	0.68	−0.04
A. afarensis	−4.20	3.40	−0.17	−1.59	5.05	3.49	0.27	2.12

	MRL3 residuals				BM residuals			
	CA1	CA2	CA3	CA4	CA1	CA2	CA3	CA4
Eigenvalue	11.26	5.79	2.25	0.27	49.56	10.31	1.58	0.34
% Variance	57.56	29.58	11.48	1.38	80.20	16.68	2.56	0.55
Can. corr.	0.96	0.92	0.83	0.46	0.99	0.95	0.78	0.51
P. paniscus	0.04	−3.89	−0.69	−1.53	3.04	−4.44	−2.08	0.62
P. troglodytes	0.15	−2.68	−1.01	0.55	4.12	−3.69	2.33	0.17
G. gorilla	−0.19	0.12	2.22	0.04	0.82	−0.81	−0.50	−1.08
P. pygmaeus	5.37	2.74	−0.94	−0.10	6.65	4.19	−0.05	0.23
H. sapiens	−5.74	2.66	−1.13	−0.09	−10.69	0.97	0.15	0.19
A. afarensis	−3.05	3.84	1.65	−2.24	−8.47	4.31	−3.33	−2.37
A. afarensis (min.)					−7.64	4.28	−1.74	−4.52
A. afarensis (max.)					−9.22	4.34	−4.77	−0.41

Abbreviations: CA, canonical axis.
Results for the analysis with BM residuals by employing minimum and maximum BM mass estimates for *A. afarensis* (see Table 1).

grounds even in the case of gorillas: although in this species this probability is higher than in other non-human hominoids, given its greater similarity to humans with regard to manual proportions, in all instances it remains below 0.05 and must be therefore discarded. Overall, this randomization approach shows that the results reported in the previous paragraph are not an artifact caused by mixing bones from several individuals, so that the conclusions derived from them are robust enough against taphonomical uncertainties surrounding the reconstruction of the *A. afarensis* hand. It can be therefore concluded that *A. afarensis* possessed human-like hands with regard to overall manual proportions even if the bones investigated do not belong to a single individual.

Relative thumb length

Measures of absolute and relative size of the first and third manual rays of *A. afarensis*, as compared with those of the extant great apes and humans, have been reported in Table 8 and Figs. 4 and 5. When absolute length is considered, the first manual ray of *A. afarensis* is shorter than in living humans, being more comparable with that of the chimpanzees, whereas the manual ray length in humans is more similar to gorillas and, to a lesser extent, orangutans (Fig. 5A). The third manual ray of *A. afarensis* is also shorter than that of humans, which in turn is shorter than in African apes and, especially, orangutans (Fig. 5B). When relative measurements are taken into account by

Table 3
Structure matrix corresponding to the canonical discriminant analyses reported in Table 2

	Raw data					Shape ratios			
	CA1	CA2	CA3	CA4		CA1	CA2	CA3	CA4
PP5L	0.45	0.27	0.07	0.13	MC1R	1.07	0.55	−0.24	−0.19
PP4L	0.41	0.14	−0.01	0.38	MC2R	0.11	−0.16	0.25	0.52
MC4IL	0.38	−0.11	0.35	0.03	MC3R	0.45	−0.55	1.11	1.08
PP3L	0.36	0.06	0.00	0.34	MC4R	−1.28	0.17	−0.13	−1.13
PP2L	0.36	0.18	0.05	0.28	MC5R	−0.14	0.15	−1.39	0.04
MP5L	0.35	0.17	0.22	0.08	PP1R	0.36	−0.36	0.03	0.00
MC3IL	0.32	−0.12	0.24	−0.07	PP2R	0.26	0.51	0.16	−0.24
MC2IL	0.28	−0.09	0.26	−0.08	PP3R	0.13	−1.02	−0.13	0.37
MP2L	0.26	0.04	0.15	0.09	PP4R	−0.26	0.28	0.23	−1.42
MC5IL	0.34	−0.05	0.52	0.02	PP5R	−0.37	0.82	0.37	1.19
MC1IL	0.01	0.21	0.37	0.04	MP2R	0.00	−0.30	−0.08	0.32
MP3L	0.25	−0.06	0.09	0.25	MP5R	0.02	0.40	−0.01	−0.10
PP1L	−0.11	0.12	0.09	0.19					

	MRL3 residuals					BM residuals			
	CA1	CA2	CA3	CA4		CA1	CA2	CA3	CA4
MC1Res	−0.72	0.67	0.15	−0.05	MC1BMRes	−1.11	0.68	−0.11	−0.65
MC2Res	−0.04	−0.01	−0.25	−0.37	MC2BMRes	0.06	0.03	−0.64	1.37
MC3Res	3.40	1.16	0.93	0.57	MC3BMRes	−0.95	−0.66	−2.08	1.19
MC4Res	0.23	−0.19	0.22	0.31	MC4BMRes	1.71	−0.18	0.42	−1.15
MC5Res	−0.03	−0.15	0.94	0.49	MC5BMRes	0.46	−0.51	1.28	−1.33
PP1Res	−0.48	−0.22	−0.06	0.30	PP1BMRes	−0.61	−0.60	0.71	−0.16
PP2Res	0.27	0.58	−0.05	0.14	PP2BMRes	0.05	0.76	0.22	0.76
PP3Res	2.38	0.67	0.52	0.91	PP3BMRes	0.56	−0.79	1.04	−0.06
PP4Res	0.16	0.28	−0.17	0.92	PP4BMRes	−0.83	1.03	1.45	0.30
PP5Res	0.31	0.53	−0.05	−1.23	PP5BMRes	0.54	1.37	−1.91	−0.33
MP2Res	0.06	−0.19	0.07	−0.10	MP2BMRes	0.10	−0.06	−0.85	0.29
MP3Res	3.07	1.46	1.16	1.19	MP3BMRes	0.62	−1.13	0.60	−0.06
MP5Res	0.25	0.22	0.43	0.14	MP5BMRes	−0.46	0.13	0.07	−0.12

Abbreviations: CA, canonical axis; MC, metacarpal; PP, proximal phalanx; MP, middle phalanx; L, absolute length; R, shape ratio relative to third manual ray length; Res, allometric residual relative to third manual ray length; BMRes, allometric residual relative to body mass.

considering intrinsic hand proportions, similar results are obtained irrespective of whether ratios (Fig. 5C) or residuals relative to third manual ray length (Figs. 4C and 5D) are employed. Thus, among extant great apes, gorillas have somewhat elongated thumbs in relative length, when compared with other African apes and, especially, with orangutans; *A. afarensis*, however, is much closer to the modern human condition, displaying a much more elongated thumb than gorillas, nearly as much as in living humans.

Separate allometric regressions for metacarpals and proximal phalanges (Figs. 4A and B,

respectively) confirm that the first manual ray in humans and *A. afarensis* has been uniformly elongated in relative terms. In the case of measurements involving the third manual ray, considerable extrapolation outside the great ape regression is necessary in order to compare them with humans and *A. afarensis*. This is not a problem, however, as shown by the fact that the inclusion of gibbons in the regression line (Figs. 4A–C) does not modify it in any significant way. Finally, when body size-scaling effects are taken into account by means of body mass residuals (Figs. 4D and 5E, F) separately for first and third manual rays, it

Table 4
Matrix of Mahalanobis square distances (D^2) for extant hominoid genera and *A. afarensis* (in the case of distances based on BM residuals, average BM estimation on the basis of human regressions, as well as minimum and maximum BM estimates have been included; see Table 1)

Raw data							Shape ratios					
	B	C	G	O	H	A		B	C	G	O	H	A
B	0.00						B	0.00					
C	4.63	0.00					C	4.12	0.00				
G	24.94	15.95	0.00				G	25.71	15.82	0.00			
O	74.12	62.70	49.83	0.00			O	41.39	32.04	23.25	0.00		
H	78.81	77.11	62.41	169.13	0.00		H	103.84	101.61	78.46	143.94	0.00	
A	61.08	61.31	34.68	109.11	12.03	0.00	A	87.22	85.54	44.98	84.03	22.84	0.00

MRL3 residuals							BM residuals					
	B	C	G	O	H	A		B	C	G	O	H	A
B	0.00						B	0.00					
C	5.89	0.00					C	21.37	0.00				
G	27.05	18.63	0.00				G	23.50	28.81	0.00			
O	74.54	57.06	47.72	0.00			O	91.81	74.31	61.02	0.00		
H	78.55	63.66	48.50	123.47	0.00		H	222.76	245.75	137.55	311.07	0.00	
A	75.31	67.67	27.57	83.42	21.02	0.00	A	219.44	261.00	122.08	246.06	34.78	0.00
							A (min.[a])	216.65	240.55	110.83	229.71	46.05	7.81
							A (max.[a])	235.57	293.23	145.92	274.55	38.12	6.48

Abbreviations: B, bonobos; C, chimpanzees; G, gorillas; O, orangutans; H, humans; A, *A. afarensis*.
[a]See note in Table 2.

Table 5
Summary of the results of canonical discriminant analyses, including percentage of correctly classified cases among extant taxa, and classification and Mahalanobis *D* square distances for *A. afarensis*

	% Correctly classified		Classification at first instance		Classification at second instance	
		Probability	Taxon	D^2	Taxon	D^2
Raw data	90.3%	0.017	Human	12.03	Gorilla	34.68
Shape ratios	91.0%	0.000	Human	22.84	Gorilla	44.98
MR3 residuals	92.2%	0.000	Human	21.02	Gorilla	27.57
BM residuals	95.0%	0.000	Human	34.78	Gorilla	122.08
BM residuals (min.[a])	95.0%	0.000	Human	46.05	Gorilla	110.83
BM residuals (max.[a])	95.0%	0.000	Human	38.12	Gorilla	145.92

[a]See note in Table 2.

emerges that more differences can be found with regard to the latter. Thus, humans differ from great apes by having somewhat elongated thumbs relative to body mass (although the difference from orangutans is not statistically significant), but the enhanced thumb/hand relationships of humans basically emerges from the considerably shortened third manual ray in relative terms, which among extant great apes is longest in orangutans and shortest in gorillas. The results for *A. afarensis*, although less secure due to body mass estimation uncertainties, suggest that no significant thumb elongation is present, although neither thumb reduction nor thumb elongation can be excluded when the uncertainty range of BM estimation, as measured from maximum and minimum BM

Table 6
Allometric regression equations (least-squares) derived in this article to compute logarithmic residuals of metacarpal, phalangeal and manual ray relative lengths, in relation to both third manual ray length and body mass

Taxon	N	y	x	r	Slope	Intercept
GA	8	ln MCL1	ln MRL3	0.728	0.82	−0.54
GAH	10	ln MCL2	ln MRL3	0.995	0.89	−0.18
GAH	10	ln MCL3	ln MRL3	0.995	0.87	−0.06
GAH	10	ln MCL4	ln MRL3	0.990	1.14	−1.54
GAH	10	ln MCL5	ln MRL3	0.969	1.12	−1.53
GA	8	ln PPL1	ln MRL3	0.674	0.50	0.63
GAH	10	ln PPL2	ln MRL3	0.919	0.99	−1.24
GAH	10	ln PPL3	ln MRL3	0.966	1.01	−1.19
GAH	10	ln PPL4	ln MRL3	0.944	1.08	−1.66
GAH	10	ln PPL5	ln MRL3	0.914	1.21	−2.52
GAH	10	ln MPL2	ln MRL3	0.986	1.08	−2.18
GAH	10	ln MPL3	ln MRL3	0.991	1.07	−1.89
GAH	10	ln MPL4	ln MRL3	0.989	1.11	−2.17
GAH	10	ln MPL5	ln MRL3	0.938	1.37	−3.79
GA	8	ln MRL1	ln MRL3	0.743	0.73	0.42
GAH	10	ln MC1	ln BM	0.749	0.16	3.15
GAH	10	ln MC2	ln BM	0.406	0.11	4.03
GAH	10	ln MC3	ln BM	0.339	0.09	4.10
GAH	10	ln MC4	ln BM	0.363	0.13	3.87
GAH	10	ln MC5	ln BM	0.476	0.18	3.60
GAH	10	ln PP1	ln BM	0.640	0.14	2.78
GAH	10	ln PP2	ln BM	0.376	0.12	3.47
GAH	10	ln PP3	ln BM	0.296	0.09	3.73
GAH	10	ln PP4	ln BM	0.310	0.10	3.63
GAH	10	ln PP5	ln BM	0.306	0.11	3.35
GAH	10	ln MP2	ln BM	0.418	0.13	2.96
GAH	10	ln MP3	ln BM	0.377	0.12	3.21
GAH	10	ln MP4	ln BM	0.383	0.13	3.15
GAH	10	ln MP5	ln BM	0.436	0.19	2.60
GAH	10	ln MR1	ln BM	0.832	0.18	3.56
GAH	10	ln MR3	ln BM	0.356	0.13	4.69

All regressions were derived for great apes and humans, except for first metacarpal and phalanx.
    Abbreviations: *y*, dependent variable; *x*, independent variable; *r*, correlation coefficient; *p*, significance; GAH, great apes and humans; GA, great apes only (modern humans excluded).

estimates for AL 333 locality, is taken into account. On the contrary, it remains clear that the third manual ray in *A. afarensis* is already reduced at least to an extent fully comparable with that of modern humans. In fact, hand reduction relative to BM in *A. afarensis* is apparently more extreme than human's average condition, or at least comparable to human's average condition (when extreme BM estimates are considered).

Randomization results for these bivariate comparisons (see Table 9) indicate that, for both ratios and third manual ray residuals, great ape proportions cannot be obtained from a chimeric human hand ($p<0.001$). Similarly, the possibility of obtaining a thumb/hand relationship within the human 95% confidence interval from a chimeric great ape hand can also be dismissed on statistical grounds ($p<0.05$). This permits a secure refutation of Susman's (1998) criticism, according to which relative thumb length would have no practical use for this fossil species because the bones could belong to several individuals. On the contrary, our randomization results indicate that the relative thumb proportions of this taxon are clearly human-like even if the bones investigated belong to many different individuals. Since humans

Table 7
Randomization results for the canonical analyses, obtained from samples of 1000 chimeric hands for each species

Raw data	B	C	G	O	H	A
B*	0.615	0.293	0.077	0.014	0.001	0.000
C*	0.339	0.454	0.142	0.051	0.014	0.000
G*	0.199	0.135	0.499	0.089	0.078	0.007
O*	0.099	0.034	0.064	0.803	0.000	0.000
H*	0.003	0.000	0.010	0.000	0.987	0.457
Ratios	B	C	G	O	H	A
B*	0.599	0.307	47	0.047	0.000	0.000
C*	0.335	0.434	0.114	0.101	0.016	0.000
G*	0.161	0.114	0.466	0.169	0.090	0.016
O*	0.137	0.041	0.118	0.704	0.000	0.000
H*	0.006	0.003	0.036	0.000	0.955	0.478
MRL3 residuals	B	C	G	O	H	A
B*	0.670	0.250	0.061	0.011	0.008	0.000
C*	0.335	0.490	0.107	0.025	0.043	0.007
G*	0.205	0.121	0.510	0.052	0.112	0.033
O*	0.037	0.065	0.048	0.838	0.012	0.004
H*	0.011	0.011	0.019	1	0.958	0.560
BM residuals	B	C	G	O	H	A
B*	0.540	0.327	0.120	0.013	0.000	0.000
C*	0.247	0.520	0.124	0.053	0.056	0.000
G*	0.235	0.237	0.324	0.097	0.107	0.013
O*	0.019	0.073	0.053	0.851	0.004	0.000
H*	0.002	0.004	0.048	0.000	0.946	0.432

In the case of extant species, the reported figures represent the probability of a chimeric hand from a certain hominoid species being classified as a given extant species. In the case of *A. afarensis*, the reported figures represent the probability of a chimeric hand from a certain hominoid species being classified like the *A. afarensis* composite hand (i.e. as a human) with comparable (equal or greater) degree of similarity (on the basis of Mahalanobis square distances).

Abbreviations: *, chimeric hand; rest as in Table 4.

display the most extreme condition of thumb length relative to third manual ray, and the condition of *A. afarensis* is derived toward the human condition, but less extreme, the probability of finding great ape chimeric hands as similar to the human condition as the *A. afarensis* hand, equals in this case the probability of finding great ape chimeric hands with a relative thumb length as high as that in *A. afarensis*. This probability can be rejected on statistical grounds ($p<0.05$) in all great ape species, except for residuals in the case of gorillas, where the probability is nevertheless very low ($p=0.068$). When BM residuals are taken into account in the case of the first manual ray, it

emerges that it is not possible to exclude on statistical grounds neither the possibility of obtaining human-like proportions from chimeric great ape hands nor great ape-like proportions from human chimeric hands. This, combined with the uncertainties in BM estimates, makes it impossible to decipher whether *A. afarensis* has a somewhat hypertrophied thumb, as with modern humans, or not. On the contrary, in the case of the third manual ray, great ape-like proportions cannot be obtained from chimeric human hands ($p<0.001$), and the possibility of obtaining human-like proportions from chimeric ape hands can be rejected in all instances ($p<0.05$) except for gorillas, where the probability is nevertheless very low ($p=0.062$). However, when the degree of similarity between *A. afarensis* and the average modern human condition is taken into account, the possibility of obtaining similar proportions by chance from a gorilla chimeric hand can be dismissed on statistical grounds ($p<0.05$). Overall these results confirm that, even if the bones employed do not belong to a single individual, *A. afarensis* has human-like thumb/hand proportions, and that these proportions, as in modern humans, mainly emerge from hand shortening instead of thumb elongation relative to BM.

Discussion

Our results confirm the previous assertions that the thumb/hand proportions in *A. afarensis* are higher than in chimpanzees (Bush, 1980; Marzke, 1983, 1997), and also indicate that this proportion is not intermediate between apes and humans, but much more closer (if not equal) to the modern human condition, irrespective of whether ratios or residuals are employed to quantify it. This indicates, contra Marzke (1997), that the thumb of *A. afarensis* was probably long enough to permit pad-to-pad precision grip. When body size-scaling effects are taken into account, we show that modern humans display a somewhat elongated thumb (at least with respect to African apes), but unfortunately this condition cannot be actually ascertained for *A. afarensis*. Nevertheless, it is clear from our results that in both cases human-like

Table 8

Descriptive statistics, ANOVA results and post-hoc multiple comparisons (Bonferroni) for absolute and relative measures of first and third manual rays on living taxa, and descriptive statistics for *A. afarensis* also (*p*-values below 0.05 indicate significant differences)

MR1L								ANOVA: F=19.962 (p=0.000)				
Taxon	N	Mean	SE	95% CI		Range		Bonferroni				
P. paniscus	20	63.26	0.81	61.57	64.95	56.5	69.0	B	C	G	O	H
P. troglodytes	59	66.86	0.92	65.02	68.70	36.2	80.9	B –				
G. gorilla	76	75.50	1.15	73.20	77.80	43.3	92.9	C 0.729	–			
P. pygmaeus	40	71.06	1.14	68.75	73.37	61.6	87.6	G 0.000	0.000	–		
H. sapiens	56	75.61	0.80	74.01	77.21	61.8	91.8	O 0.003	0.085	0.036	–	
A. afarensis	1	65.6	–	–	–	–	–	H 0.000	0.000	1.000	0.049	–

MR3L								ANOVA: F=132.848 (p=0.000)				
Taxon	N	Mean	SE	95% CI		Range		Bonferroni				
P. paniscus	18	180.85	2.48	175.61	186.09	160.7	205.1	B	C	G	O	H
P. troglodytes	58	188.64	2.21	184.21	193.07	116.3	220.1	B –				
G. gorilla	68	189.06	2.32	184.43	193.70	152.1	230.4	C 0.769	–			
P. pygmaeus	41	214.36	2.89	208.53	220.20	186.5	259.6	G 0.576	1.000	–		
H. sapiens	51	139.69	1.35	136.98	142.41	118.5	160.3	O 0.000	0.000	0.000	–	
A. afarensis	1	126.0	–	–	–	–	–	H 0.000	0.000	0.000	0.000	–

MR1Rat								ANOVA: F=417.615 (p=0.000)				
Taxon	N	Mean	SE	95% CI		Range		Bonferroni				
P. paniscus	17	0.35	0.00	0.34	0.36	0.31	0.37	B	C	G	O	H
P. troglodytes	56	0.35	0.00	0.35	0.36	0.19	0.45	B –				
G. gorilla	67	0.40	0.00	0.39	0.41	0.25	0.46	C 1.000	–			
P. pygmaeus	40	0.33	0.00	0.32	0.34	0.29	0.39	G 0.000	0.000	–		
H. sapiens	49	0.54	0.00	0.54	0.55	0.50	0.69	O 0.187	0.002	0.000	–	
A. afarensis	1	0.52	–	–	–	–	–	H 0.000	0.000	0.000	0.000	–

MR1Res								ANOVA: F=175.178 (p=0.000)				
Taxon	N	Mean	SE	95% CI		Range		Bonferroni				
P. paniscus	17	−0.04	0.01	−0.07	−0.01	−0.15	0.03	B	C	G	O	H
P. troglodytes	56	−0.02	0.01	−0.05	0.00	−0.64	0.14	B –				
G. gorilla	68	0.10	0.01	0.08	0.12	−0.38	0.23	C 1.000	–			
P. pygmaeus	40	−0.05	0.01	−0.07	−0.03	−0.18	0.10	G 0.000	0.000	–		
H. sapiens	49	0.33	0.01	0.32	0.34	0.26	0.52	O 1.000	1.000	0.000	–	
A. afarensis	1	0.26	–	–	–	–	–	H 0.000	0.000	0.000	0.000	–

MR1BMRes								ANOVA: F=8.853 (p=0.000)				
	N	Mean	SE	95% CI[a]		Range[a]		Bonferroni				
P. paniscus	9	−0.06	0.02	−0.10	−0.01	−0.17	0.01	B	C	G	O	H
P. troglodytes	9	−0.01	0.02	−0.07	0.04	−0.12	0.11	B –				
G. gorilla	12	−0.02	0.02	−0.06	0.02	−0.12	0.07	C 1.000	–			
P. pygmaeus	15	0.02	0.02	−0.02	0.06	−0.09	0.12	G 1.000	1.000	–		
H. sapiens	17	0.09	0.02	0.05	0.12	−0.07	0.21	O 0.089	1.000	1.000	–	
A. afarensis	1	−0.07	–	−0.10	−0.03	−0.19	0.07	H 0.000	0.005	0.001	0.066	–

[a]95% CI and range for body mass residuals in *A. afarensis* were computed by taking into account, respectively, the 95% CI for the average body mass estimates (human regressions) and the maximum and minimum body mass estimates (both human and hominoid regressions).

Table 8   (continued)

MR3BMRes								ANOVA: F=101.024 (p=0.000)				
Taxon	N	Mean	SE	95% CI[a]		Range[a]		Bonferroni				
P. paniscus	9	0.03	0.02	−0.01	0.07	−0.02	0.14	B	C	G	O	H
P. troglodytes	9	0.08	0.02	0.04	0.12	0.02	0.18	B –				
G. gorilla	12	−0.04	0.02	−0.08	0.00	−0.12	0.07	C 1.000	–			
P. pygmaeus	15	0.19	0.02	0.15	0.23	0.10	0.31	G 0.100	0.001	–		
H. sapiens	17	−0.25	0.02	−0.28	−0.21	−0.42	−0.14	O 0.000	0.002	0.000	–	
A. afarensis	1	−0.36	–	−0.38	−0.33	−0.45	−0.26	H 0.000	0.000	0.000	0.000	–

Abbreviations: N, sample size; SE, standard error; CI, confidence interval for the mean; other abbreviations as in Tables 3 and 4.

thumb/hand proportions basically result from finger shortening, instead of thumb elongation, thus confirming the previous analyses of Latimer (1991) and Watkins et al. (1993, 1996). Although the latter conclusion might seem especially tentative because it is based on body mass estimates from different specimens of locality AL 333, in fact it is sufficiently robust against BM estimation uncertainties (as measured by maximum and minimum estimates derived for this locality). Moreover, we further extend previous results by showing that *A. afarensis* not only displays human-like thumb/hand proportions, but also overall manual proportions, irrespective of whether ratios or logarithmic residuals are employed to quantify them. These results are in accordance with the fact that thumb/hand proportions similar to that of modern man have been reported for the nearly complete hand of *A. africanus* (Clarke, 1999), which has been found in anatomical connection. Finally, our randomization approach confirms that all the above-mentioned conclusions stand even if the bones employed do not belong to a single individual, thus making irrelevant the criticism previously raised by Susman (1998).

Our results contradict the current paleoanthropological paradigm (Susman, 1994, 1995, 1998) according to which human-like thumb/hand proportions would be diagnostic of stone tool-making capacities. This was based on the work of Napier (1960, 1962a,b), who identified anatomical correlates of precision grasping activities in primate hands that were later employed to infer the capabilities of fossil hominine hands in the cultural realm of tool-use and tool-making (e.g. Napier,

1962b; Susman, 1994, 1998). In fact, according to Napier (1962b, p. 411), precision grip would not have been an essential requisite for the Oldowan (Mode I) technology, although others have later disagreed, arguing that both a strong power grip and a strong precision grip would have been required (Toth and Schick, 1993). Be that as it may, since the human-like manual proportions of *A. afarensis* predate the earliest lithic industries found in the archeological record by about 1 Myr, it seems clear that the criterion of historical concordance is not fulfilled for the null hypothesis being tested in this article. Accordingly, it is possible to confidently refute that human-like manual proportions originally evolved as an adaptation for stone tool-making. This does not exclude at all that other features of the human hand were selected to serve this function, but with regard to manual proportions, stone tool-making would have only favored minor readjustments at most. It would be simply a more ancient acquisition, later co-opted to serve this new function (although original pressures need not be necessarily entirely different if based on other tool-related behaviors). With regard to stone tool-making, the proportions of the human hand would not be an adaptation, but an exaptation (sensu Gould and Vrba, 1982), and the hypothesis that human-like precision grasping equates to stone tool-making must be rejected. According to some authors, even though anatomical traits might permit prehensile actions suitable for certain behaviors such as stone tool-making, it is the brain with its associated cognitive abilities that, in ultimate terms, governs their execution. In Napier's (1956, p. 913) words: "it is
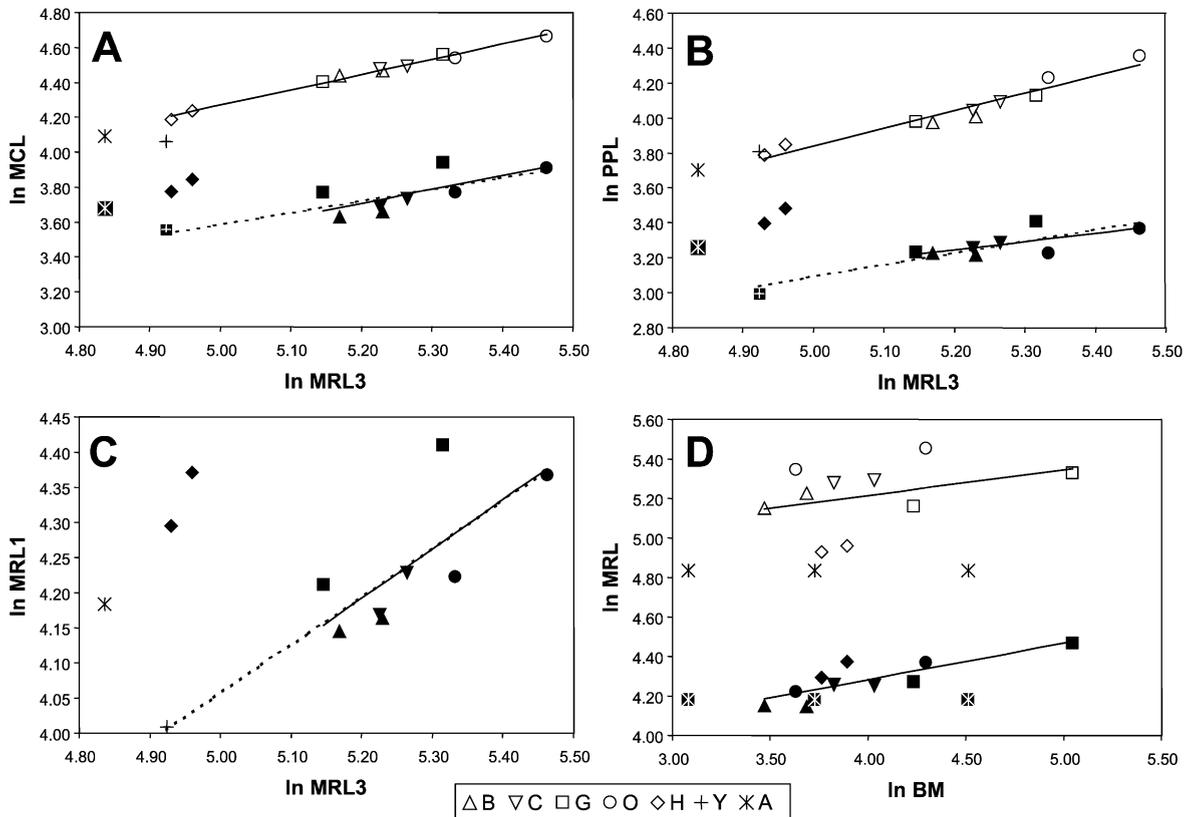
Fig. 4. Allometric regression equations (least-squares). (A) Length of first and third metacarpals vs. third manual ray length; (B) length of first and third proximal phalanges vs. third manual ray length; (C) first vs. third manual ray length and (D) length of first and third manual rays vs. body mass. Open symbols: third manual ray; solid symbols: first manual ray. Continuous lines: great ape (third manual ray) or great ape and human (first manual ray) regressions; discontinuous lines: hominoid regression including gibbons (only for third manual ray). Abbreviations: Y, *H. lar*; rest as in Fig. 3.

in the elaboration of the central nervous system and not in the specialization of the hand that we find the basis of human skill". In any case, our results indicate that alternative explanations for the emergence of human-like manual proportions during evolution must be therefore sought (see subsequently).

One possible hypothesis would be that human-like manual proportions originally evolved as a result of manipulative behaviors exceeding those reported among extant non-human primates, a proposal that can be currently neither supported nor refuted on the basis of the archeological record. According to this, early hominines would have displayed tool-related behaviors more sophisticated than those reported for wild chimpanzees,

including tool-use and perhaps also tool-making with organic raw material. Marzke (1997, p. 105), in particular, defines four stages in the evolution of tool-behavior. The first stage, which corresponds to the use and modification of natural objects with hands primarily adapted for locomotion, as in chimpanzees, would have presumably been already present in the last common ancestor of apes and humans. The second stage, attributed by Marzke (1997) to *A. afarensis*, would already imply an increasing use of natural objects of various sizes and shapes as tools, as facilitated by new and distinctively human morphological features (albeit excluding pad-to-pad precision grasping according to her account). According to this author, the longer thumb of *A. afarensis* in comparison to
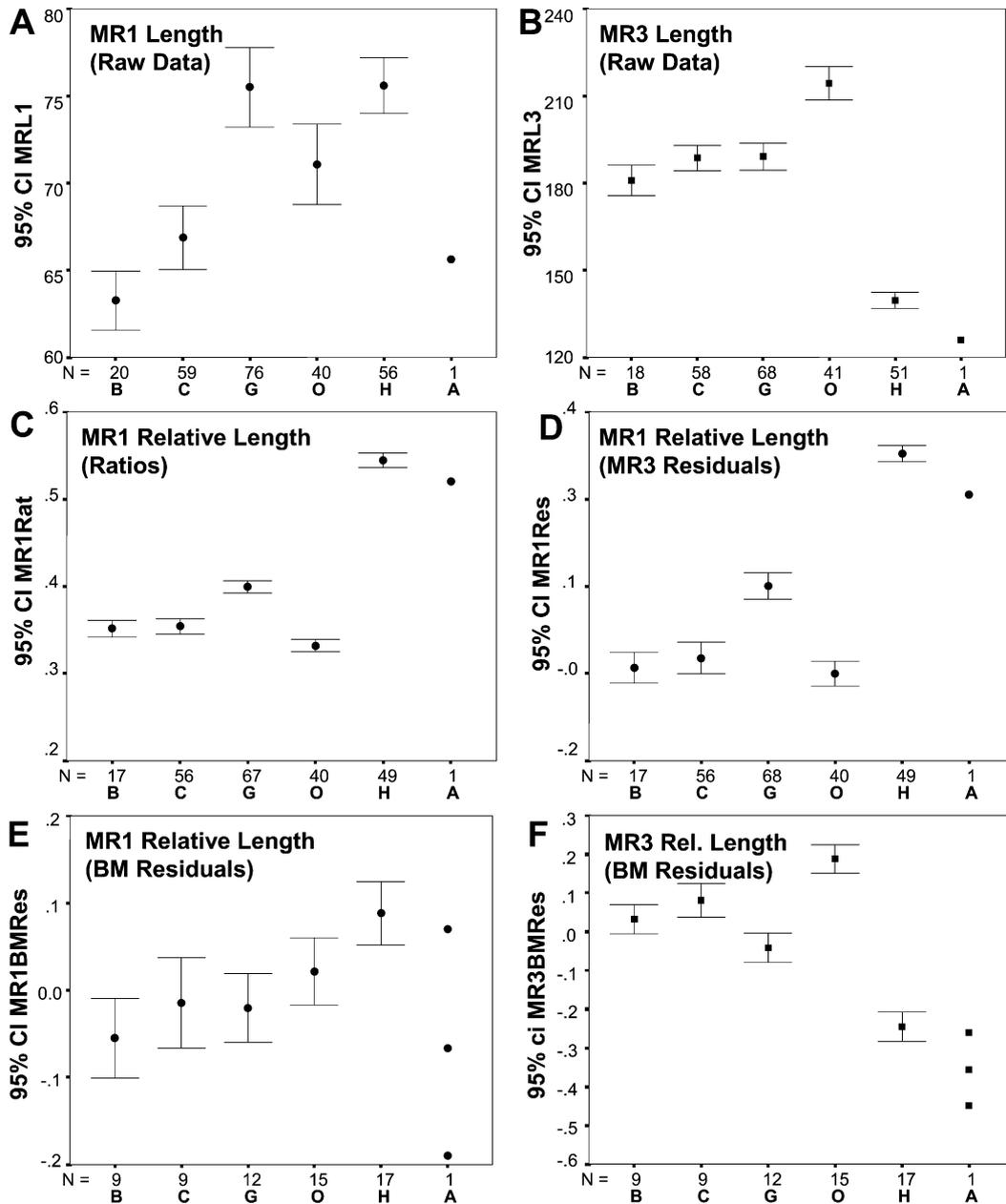
Fig. 5. Plot of mean values and 95% confidence intervals for the mean of the raw data (length of first and third manual rays), ratios (relative length of first manual ray), and residuals (length of first manual ray relative to length of third manual ray, and length of first and third manual rays relative to body mass). In the case of BM residuals in *A. afarensis*, reported values are based on average BM estimate (human regression) as well as maximum and minimum BM estimates (human and hominoid regressions). Abbreviations: B, *P. paniscus*; C, *P. troglodytes*; G, *G. gorilla*; O, *P. pygmaeus*; H, *H. sapiens*; A, *A. afarensis*.

Table 9
Randomization results for the comparison of ratios and residuals between *A. afarensis* and extant hominoids, obtained from samples of 1000 chimeric hands for each species

MR1Rat	B	C	G	O	H	A
B*	0.325	0.300	0.032	0.169	0.000	0.000
C*	0.251	0.226	0.066	0.130	0.001	0.001
G*	0.101	0.097	0.120	0.040	0.005	0.011
O*	0.076	0.148	0.024	0.177	0.000	0.000
H*	0.000	0.000	0.000	0.000	0.143	0.656
MR1Res	B	C	G	O	H	A
B*	0.327	0.368	0.014	0.258	0.000	0.000
C*	0.246	0.279	0.089	0.175	0.001	0.004
G*	0.083	0.091	0.169	0.056	0.012	0.068
O*	0.219	0.221	0.058	0.181	0.000	0.001
H*	0.000	0.000	0.001	0.000	0.144	0.799
MR1BMRes	B	C	G	O	H	A
B*	0.561	0.491	0.407	0.203	0.032	0.554
C*	0.434	0.465	0.373	0.268	0.063	0.570
G*	0.271	0.233	0.184	0.134	0.081	0.372
O*	0.292	0.353	0.263	0.255	0.195	0.714
H*	0.118	0.288	0.201	0.312	0.379	0.974
MR3BMRes	B	C	G	O	H	A
B*	0.591	0.362	0.231	0.011	0.000	0.000
C*	0.525	0.514	0.132	0.004	0.011	0.004
G*	0.151	0.077	0.337	0.002	0.062	0.024
O*	0.112	0.249	4	0.370	0.000	0.000
H*	0.000	0.000	0.000	0.000	0.506	0.528

In the case of extant species, the reported figures represent the probability of a chimeric hand from a certain hominoid species of falling within the 95% CI for the mean of that species. In the case of *A. afarensis*, the reported figures represent the probability of a chimeric hand from a certain hominoid species being equally or more similar than the *A. afarensis* composite hand to the average of its most similar extant hominoid species (humans); note that, in the case of MR1 ratios and residuals, the reported probability for *A. afarensis* also equals the probability of sampling in an extant great ape species a relative thumb length as high as that of *A. afarensis*.

Abbreviations are as in Table 7.

chimpanzees "should have provided an advantage in securing and controlling flakes with the middle and distal segments of the flexed fingers in the pad-to-side grip, and in holding relatively large stones by the three-jaw chuck grip" (Marzke, 1997, p. 105). Our finding that, with regard to thumb/hand proportions, *A. afarensis* would have been most likely also capable of human-like pad-to-pad precision grasping would be compatible with Marzke's (1997) hypothesis as well.

Another possible explanation for the emergence of human-like manual proportions in early australopiths is however possible, being based on the fact that, besides tool-use and tool-making, the hands of primates serve a wide range of different functions, both locomotor and manipulative. Our anthropocentric perspective makes it difficult to realize that manipulation in fossil hominines must not be necessarily equated with tool-behavior. All primates employ their hands for different manipulative purposes, including harvesting, foot-processing and grooming, much more frequently than other mammals and sometimes involving complex movements in spite of being unrelated with tools. It is our contention that the origin of human hand morphology should not be discussed exclusively in the light of tool-related behaviors, for this would lead to circular reasoning, so that the link between tool-related behaviors and human manual proportions would become an inevitable conclusion. Rather, other manual activities performed by non-human primates in non-locomotor contexts, and involving complex manipulation, should be appropriately taken into account. In extant non-human primates, the extent of manipulative adaptations is restricted to some degree by the biomechanical constraints imposed by locomotion. Depending on the type of locomotion, this can preclude the acquisition of the optimal manual proportions for more efficient manipulation. According to Preuschoft and Chivers (1993, p. 2), "primates seem to acquire their hand shape with respect to locomotion and to make the best of it when in the need of performing precise manipulations" because "locomotion … evokes higher external forces against a hand than most sorts of 'precision handling' ". More precisely, according to Jouffroy (1991, p. 21), "the forces involved in prehensile activity are far weaker, more variable in their direction, and more casual than the positional forces. Thus, primate hands, like those of other mammals, remain shaped predominantly according to the highly selective biomechanical constraints of locomotion". Thus, although manipulation and locomotion are not excluding functions, they pose different and frequently opposed selection pressures on hand morphology. And even though manipulation selection pressures

are present in non-human primates, as a result of the constraints imposed by locomotion, they are less reflected in hand morphology than might be expected solely on its own grounds.

The locomotor constraints on hand proportions will be more or less incompatible with enhanced manipulative capabilities depending on the type of locomotion. Thus, the manual proportions of hindlimb-dominated, quadrupedal monkeys are generally more similar to those of humans than to those of apes, especially in gelada (*Theropithecus gelada*), where the index finger is very short and the thumb relatively long, resulting in an " 'opposability-index' … higher than in man" (Maier, 1993). In geladas this might be at least partially related to the manipulative activities that this taxon displays during feeding, but the connection with terrestrial quadrupedalism is also clear: both geladas and baboons (which utilize digitigrade positions on the ground) display relatively short hands, just like the terrestrial quadruped *Erythrocebus*, whereas the arboreal quadrupeds *Macaca* and *Cercopithecus* display longer hands (Maier, 1993). In other words, terrestrial quadrupedalism in monkeys would favor a short hand, thus being compatible with an enhanced thumb/hand relationship more similar to that of humans. On the contrary, the forelimb-dominated climbing and suspensory behaviors of hominoids, even in the knuckle-walking African apes, favor a long hand that is thus less well suited for manipulative functions. In some instances, this locomotor specialization would have proceeded at the expense of some manipulative skills, as in gibbons, whereas in other instances hand morphology would represent some compromise between manipulative and locomotor functions, as in chimpanzees (Boesch and Boesch, 1993). Only committed terrestrial bipedalism like that found in modern humans, however, frees the hands from locomotor stresses and leaves them exclusively subject to manipulative selection pressures.

The significance of bipedalism for the emergence of modern human manipulative skills has been recognized ever since Darwin (1871, p. 51), according to whom "the hands and arms could hardly have become perfect enough to have manufactured weapons … as long as they were habitually used for locomotion". The same viewpoint is expressed by Jouffroy (1991, p. 21), according to which "Complete unloading from body weight support and locomotor forces, as a consequence of bipedalism, was the prerequisite for developing the unique dexterity and sensitivity that characterizes the human hand". Most recently, this relationship has been also advocated by Hartwig and Doneski (1998, p. 402), who assert that the "evolution of precision manipulation is the story of bipedalism, relaxed selection on upper limb joint stability, and the exploitation of progressive efficiency in the application of a preadapted biobehavioral grasping complex". Here, we propose the hypothesis that human manual proportions, including an increased thumb/hand relationship, could have simply originally emerged once the hands were freed from locomotor demands by the adoption of bipedal locomotion, merely as a result of the same manipulative selection pressures that can be found among extant non-human primates. In other words, with the acquisition of habitual terrestrial bipedalism, the hands of early hominines would have become essentially unconstrained by locomotor demands, thus being (mostly or entirely) subject to manipulative selection pressures. This agrees with evidence from *A. afarensis*, which besides human-like manual proportions, already displays many adaptations to committed bipedalism, some of which imply a decrease in climbing efficiency (see discussion below). This is further supported by the fact that the increased thumb/hand proportions in this taxon were not attained by lengthening the thumb (as would be expected if the hand was still under forelimb-dominated locomotor selection pressures) but rather by reducing the length of the hand (as would be expected if the hand was no longer under significant locomotor pressures). This suggests that the relaxation of locomotor selection pressures could be the basic factor leading to the evolution of human-like manual proportions, since a reduction of finger length would be disadvantageous for arboreal locomotor behaviors such as climbing and suspension.

Bipedalism in early australopiths is documented beyond any reasonable doubt, not only by anatomical evidence, but also by the fossil footprints

of Laetoli from about 3.5 Ma (Leakey et al., 1976; Leakey and Hay, 1979; White, 1980), which are very modern in appearance (Clarke, 1979; Leakey and Hay, 1979; Day and Wickens, 1980; Charteris et al., 1981, 1982; Tuttle, 1985; White and Suwa, 1987) and have been attributed by some authors to *A. afarensis* (White and Suwa, 1987). The type and frequency of australopithecine bipedalism in comparison with that of living humans, however, has been vigorously discussed. The discussion has been centered around whether early australopiths were committed terrestrial bipeds, like modern humans (Robinson, 1972; Lovejoy et al., 1973, 1996; Lovejoy, 1974, 1988; Gomberg and Latimer, 1984; Latimer et al., 1987; Latimer and Lovejoy, 1989, 1990a,b; Latimer, 1991; Ohman et al., 1997), or rather displayed a more primitive type of bipedalism combined with some degree of arboreal climbing and/or suspension (Vrba, 1979; Prost, 1980; Jungers and Stern, 1983; Stern and Susman, 1983, 1991; Susman et al., 1984, 1985; Senut and Tardieu, 1985; McHenry, 1986; Senut, 1991; Susman and Stern, 1991; Hunt, 1994; Abitbol, 1995; Clarke and Tobias, 1995; Berger and Tobias, 1996). These opposing views are not a problem of lack of appropriate fossil material, but rather a matter of interpretation of the available anatomical evidence (Latimer, 1991).

The concept of total morphological (or biomechanical) pattern makes sense when trying to infer the locomotor repertoire of a fossil species (Stern and Susman, 1991), especially if we take into account that extinct animals might have displayed a combination of locomotor behaviors not matched by any living species (Rose, 1984). The interpretation of this biomechanical pattern in *A. afarensis*, however, is not straightforward; while the bipedalism-related features of this taxon can be readily interpreted as adaptations due to its derived status, the climbing-related features of the *A. afarensis* forelimb (Stern and Susman, 1983) are hominoid primitive retentions (Gebo, 1996), and hence of doubtful functional significance. Some authors interpret them on functional grounds (e.g. Stern and Susman, 1983; Susman and Stern, 1991), and others do not (e.g. Latimer, 1991). Susman and Stern (1991) contend that primitive retentions cannot be ignored, and cite as an example how

African ape morphology could be thus misinterpreted as a derived terrestrial knuckle-walking adaptation with primitive, non-functional arboreal retentions. Knuckle-walking, however, is a compromise between the needs posed by arboreal feeding/nesting and terrestrial travel (Tuttle, 1975), so that in spite of being derived, this locomotor behavior does not enter into conflict with the requirements of arboreal locomotion. In fact, the latter author has reasonably argued that if this particular type of terrestrial locomotion was favored over other types such as typical digitigrade quadrupedalism and committed bipedalism in African apes, it was precisely due to the need to preserve the long hand required by their retained, more ancient forelimb-dominated arboreal locomotion. On the contrary, many of the bipedal adaptations in *A. afarensis* already imply a concomitant decrease in the efficiency of climbing abilities, showing that "directional pressures for terrestrial bipedality had clearly overcome stabilizing selection for arboreality" by this time (Latimer, 1991, p. 172). This is particularly significant in the upper limbs, which have only minor effects on the mechanics of bipedalism, but play a primary role in arboreal locomotion. As noted by Latimer (1991), if arboreality was still significant in *A. afarensis*, due to stabilizing selection we would expect climbing adaptations to be preserved (or even exaggerated) in its hands and arms, which is not the case, thus reflecting the abandonment of the hominoid locomotor pattern of forelimb dominance in favor of a hindlimb-dominated one (Watkins et al., 1993). The fact that human-like proportions in the *A. afarensis* hand had been attained by finger length reduction thus probably indicates that "stabilizing selection for long digits had been superseded by directional pressures for shorter fingers" (Latimer, 1991, p. 174) by this time. Although relaxation of arboreal locomotor selection pressures does not mean that australopiths never climbed, it suggests that climbing behaviors were no longer an adaptively significant component in their locomotor repertoire, or were at least less significant than bipedal ones. Accordingly, relaxation of selection pressures in the hand of early australopiths can be confidently inferred.

The recent finding that the bipedal ape *Oreopithecus bambolii* (Köhler and Moyà-Solà, 1997) also displayed human-like proportions with regard to thumb/hand relationships (Moyà-Solà et al., 1999) suggests that once freed from locomotor demands, human-like manual proportions could evolve as a result of manipulative selection pressures unrelated to stone tool-making behaviors. The relationship between human-like manual proportions and bipedalism might be also partially attributable to pleiotropy, i.e. "a situation in which a single gene influences multiple phenotypic traits" (Hodgkin, 1998, p. 501). The many inductive interactions that occur between different parts of the body during embryonic development can cause mutations in one part to have pleiotropic effects in others. Pleiotropic effects between forelimbs and hindlimbs, which to a large extent share a common genetic basis, are thus conceivable, especially given the fact that the self-organizing capacity of the limb is very limited in amniotes (Galis et al., 2001). In vertebrates, limb identity is determined by quantitative and qualitative differences in *Hox* gene expression as well as the differential expression of other transcriptional regulators such as the T-box (*Tbx*) genes (Cohn and Bright, 1999). Nevertheless, the same genes from the *HoxA* and *HoxD* homeoblox clusters are expressed in the posterior parts of both fore- and hindlimb buds, with digit number and size being dependent on cumulative expression of group 11, 12 and 13 genes from the above-mentioned clusters (Zákány et al., 1997; Coates and Cohn, 1998), especially *Hoxa*-13, *Hoxd*-13, *Hoxd*-12 and *Hoxd*-11 (Zákány and Duboule, 1999). This raises the question of the role played by pleiotropy in manual and pedal hominine evolution following the adoption of bipedal locomotion. According to this possibility, with the advent of bipedal locomotion and due to a common genetic basis, the adaptive reduction in toe length could have influenced to some extent, a nonadaptive (but not necessarily maladaptive) reduction in finger length (although we must note that the reverse possibility, not considered below, may be equally plausible).

It is difficult to evaluate the potential role of pleiotropy without firm developmental evidence, but let us assume that finger reduction in *A. afarensis* is to some degree attributable to pleiotropy. Three different possibilities exist: (1) finger reduction was selectively neutral, and evolved exclusively as a result of pleiotropy; (2) finger reduction was positively selected (presumably as a result of manipulative selection pressures), so that pleiotropic effects merely reinforced finger reduction; or (3) finger reduction was negatively selected (presumably as a result of retained, arboreal locomotor behaviors), but it was nevertheless selected as a result of pleiotropic effects coupled with stronger selection pressures favoring toe reduction (and reasonably attributable to derived, terrestrial bipedalism). The first possibility seems very unlikely, for the fact that primates employ their hands in manipulation and locomotion suggests that finger reduction must have been under selection, either positively (for manipulation, if ancestral, forelimb-dominated locomotor behaviors were already adaptively insignificant or at least less significant than terrestrial bipedalism) or negatively (for locomotion, in the opposite situation). On the other hand, when the third situation, termed antagonistic pleiotropy, occurs, stabilizing selection can lead to an intermediate value for each character, resulting in the highest overall fitness (e.g. Futuyma, 1986, p. 206). This would be the case if the locomotor repertoire of *A. afarensis* combined significant amounts of both terrestrial bipedalism and arboreal climbing and/or suspension. However, since both the foot and the hand of *A. afarensis* are already considerably derived towards the modern human condition, adapted respectively for terrestrial bipedalism and manipulation, locomotor selection pressures on the forelimb had probably become less important by this time. Only the second possibility remains, in which finger reduction was positively selected for manipulation, but pleiotropic effects also contributed to it to some (currently unknown) extent. But even if we admitted the most extreme case, i.e. finger reduction entirely attributable to pleiotropy, with regard to stone tool-making human-like manual proportions would be still an exaptation. The only difference would be that human-like manual proportions would have originated as a non-adaptive by-product of bipedalism rather than an optimization for manipulative function, thus

equally highlighting the primary role of bipedalism hypothesized by us.

It should be noted, however, that the hypothesis that human-like manual proportions originally evolved as a response to the relaxation of locomotor selection pressures in the hand (coupled or not with pleiotropy) is not mutually exclusive of Marzke's (1997) hypothesis that postulates enhanced tool-related behaviors in early hominines. Both factors could have acted simultaneously, and the investigation of manual proportions and locomotion in earlier hominines such as *Ardipithecus* could, in principle, provide a test for the former hypothesis: if it could be shown that human-like manual proportions emerged before the advent of committed terrestrial bipedalism, then non-lithic tool-behaviors would be vindicated over bipedalism as the prime factor in the evolution of human hand proportions. With currently available evidence, however, it is not possible to discern between these two competing (but not necessarily exclusive) alternatives, and we must await future discoveries.

Summary and conclusions

In this article, we test the hypothesis that human-like manual proportions, including the enhanced thumb/hand relationship that permits pad-to-pad precision grasping in modern humans, originally evolved as an adaptation to stone tool-making. This hypothesis is tested by investigating the proportions of the *A. afarensis* composite hand from locality AL 333/333w (Hadar, Ethiopia) by means of bivariate and multivariate morphometric analyses. We show that human-like manual proportions can be already found in *A. afarensis*, including a thumb/hand relationship that would have most likely permitted pad-to-pad human-like precision grasping, even if the bones employed in the computations do not belong to a single individual. Since this taxon significantly predates the appearance of stone tools and cut-marks in the archeological record, this permits a secure refutation of the hypothesis that human-like manual proportions are an adaptation to stone tool-making (although they would have been later

co-opted to serve this function). Several alternative explanations for the origin of human-like hand proportions are possible. Following previous authors, these manual proportions could have been favored by manipulative behaviors in early hominines exceeding those reported among extant non-human primates (including tool-use and/or non-lithic tool-making). This hypothesis can be neither supported nor refuted on the basis of currently available evidence from the archeological record. Alternatively (but not exclusively), we propose the hypothesis that complex manipulation selection pressures already present in extant non-human primates might have been enough to favor the evolution of human-like proportions, once locomotor selection pressures imposed by forelimb-dominated locomotion were relaxed with the adoption of committed terrestrial bipedalism. Although there has been much controversy about the locomotor behavior of *A. afarensis*, this hypothesis is supported by the fact that, as in modern humans, the human-like manual proportions of this taxon are mainly attributable to shortened fingers, a feature that, like some adaptations to committed terrestrial bipedalism in this taxon, implies a decrease in the efficiency of arboreal locomotion. The hypothesis proposed here could be tested by investigating the manual proportions and locomotor behavior in earlier hominines, such as *Ardipithecus*. In any case, both tool-behavior and bipedalism could have acted synergistically in the origin of human manual proportions, and even pleiotropy cannot be currently discarded.

Acknowledgements

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