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A reassessment of the presumed Neandertal remains from San Bernardino Cave, Italy

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ABSTRACT

In 1986–1987, three human remains were unearthed from macro-unit II of San Bernardino Cave (Berici Hills, Veneto, Italy), a deposit containing a late Mousterian lithic assemblage. The human remains (a distal phalanx, a lower right third molar and a lower right second deciduous incisor) do not show diagnostic morphological features that could be used to determine whether they were from *Homo neanderthalensis* or *Homo sapiens*. Despite being of small size, and thus more similar to recent *H. sapiens*, the specimens were attributed to Neandertals, primarily because they were found in Mousterian layers. We carried out a taxonomic reassessment of the lower right third molar (LRM$_3$; San Bernardino 4) using digital morphometric analysis of the root, ancient DNA analysis, carbon and nitrogen isotope analyses, and direct accelerator mass spectrometry (AMS) radiocarbon dating of dentine collagen. Mitochondrial DNA analysis and root morphology show that the molar belongs to a modern human and not to a Neandertal. Carbon 14 (^{14}C) dating of the molar attributes it to the end of the Middle Ages (1420–1480 cal AD, 2 sigma). Carbon and nitrogen isotope analyses suggest that the individual in question had a diet similar to that of Medieval Italians. These results show that the molar, as well as the other two human remains, belong to recent *H. sapiens* and were introduced in the Mousterian levels post-depositionally.

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Introduction

In 1986–1987, three human remains were unearthed in macro-unit II of San Bernardino Cave (Berici Hills, Veneto, Italy). This late Mousterian deposit has been dated to 28–59 ka BP (thousands of years before present) through radiocarbon and electron spin resonance/U-series dating (Peresani, 2011; see Supplementary Online Material [SOM] for more details about setting, history, and archaeology of San Bernardino Cave; Figs. S1–S6; Table S1). The human remains include a distal hand phalanx (San Bernardino 3), a heavily worn lower right third molar (LRM$_3$; San Bernardino 4), and a lower right second deciduous incisor (Rdi$_2$; San Bernardino 5) (Fig. 1). All of the remains were originally described by Vacca and Alciati (2000) as belonging to *Homo neanderthalensis*, probably more for their presumed association with Mousterian levels than

for their size and morphology, which alone does not exclude them from modern humans. The small size of the elements in question was justified as a peculiarity of Southern (Mediterranean) Neandertals, thus supporting previous hypotheses by de Lumley (1973) and more recent bioinformatic models by Fabre et al. (2009), based on data from genetics, demography and palaeoanthropology.

The distal phalanx (San Bernardino 3) is extremely gracile, with a narrow apical tuft (Fig. 1). The size of this phalanx (length, tuft and base width) does not find any parallel in the Neandertal sample, and is also very small compared with recent *Homo sapiens* (Table S2). Even if worn, the San Bernardino 5 Rdi$_2$ shows a small lingual tuberosity, no evidence of a marginal ridge mesially and minimal development of the distal marginal ridge (Fig. 1). These features are shared with both Neandertals and Upper Paleolithic *H. sapiens* (Trinkaus et al., 2000). Most importantly, San Bernardino 5 has a small labiolingual breadth, almost two standard deviations from that of Neandertals, but close to the mean computed for recent *H. sapiens* (Table S3).
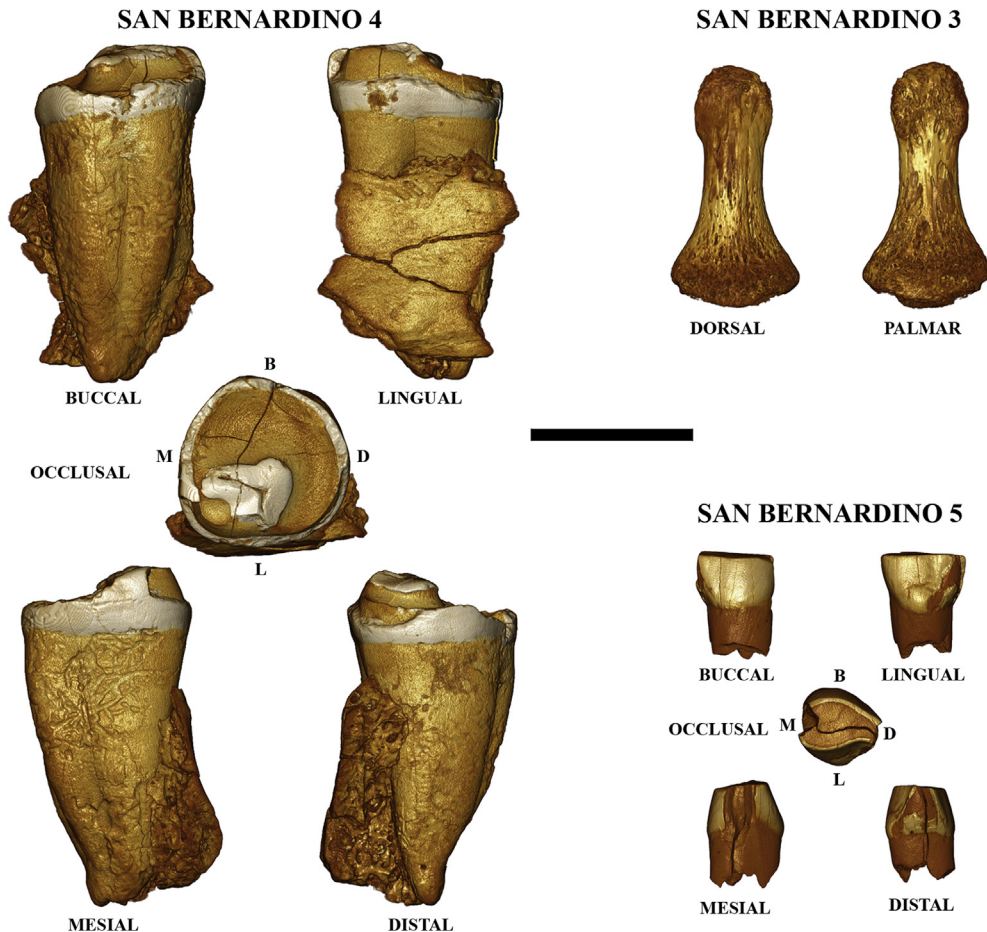
Figure 1. Three-dimensional digital models of San Bernardino 3 (distal phalanx), San Bernardino 4 (lower right third molar, LRM_3), and San Bernardino 5 (lower right second deciduous incisor, Rdi_2). The black bar in the figure is equivalent to 1 cm. B, buccal; D, distal; L, lingual; M, mesial.

Vacca and Alciati (2000) provided a thorough morphological description of San Bernardino 4, with convincing evidence that it should be considered a LRM_3 based on the shape of the crown, the shape of the pyramidal fused roots and the position of the small preserved portion of the mylohyoid line, which is close to the alveolar process of the mandible (Fig. 1). The tooth is heavily worn, thus preventing any reliable morphological and morphometric comparison of the crown. However, the authors were able to explore the pulp chamber through radiographs of the tooth, noting the absence of taurodontism, a feature typically observed in Neandertal molars (Kupczik and Hublin, 2010).

The human remains from San Bernardino Cave pose several questions that need to be answered. If the remains belong to *H. neanderthalensis*, then they would confirm the tendency towards marked skeletal 'gracilization' in Neandertals living around the Mediterranean Basin, hypothesized by de Lumley (1973) and observed by Benazzi and colleagues during the reassessment of the teeth from Taddeo cave (Benazzi et al., 2011a) and the molar Leuca I (Benazzi et al., 2013). If, on the other hand, the remains do not belong to Neandertals and the Mousterian deposit from which they originate was in situ, then they might belong to early anatomically modern humans. In this case, however, our general assumption about the biological attribution of late Mousterian tech-nocomplexes to Neandertals should be revised. The third possibility is that the fossils are the remains of recent *H. sapiens*, as strongly suggested, for instance, by the small size of the distal phalanx and of the Rdi_2 (Tables S2 and S3). If that were the case, the Mousterian

levels of the macro-unit II would have to be viewed as most likely disturbed and the skeletal materials recovered within them no longer part of the human fossil record.

In this contribution, we investigated specimen San Bernardino 4 (LRM_3) to verify whether its original attribution as a Neandertal is confirmed by state-of-the-art methods. This tooth was microCT-scanned to digitally study its root morphology; it was also sampled for ancient mtDNA, accelerator mass spectrometry (AMS) radiocarbon dating, and isotope analyses, to establish its taxonomy, age, and diet. Since San Bernardino 3 and San Bernardino 5 were discovered close to San Bernardino 4, results from the latter might be also useful to clarify the taxonomy of the other human remains.

Materials and methods

Root morphology

The molar was scanned with a Skyscan 1172 microtomographic system (mCT) (Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany) using the following scan parameters: 100 kV, 100 μA, with an aluminum/copper filter (0.50 mm/0.04 mm thickness). Volume data were reconstructed using isometric voxels of 13.21 μm. The image stack was segmented using a semiautomatic threshold-based approach in Avizo 7 (Visualization Sciences Group Inc.) to separate the enamel, the dentine and the pulp chamber and to reconstruct a 3D digital model of the tooth (Fig. 2). Since the crown is heavily worn, only the root and the pulp chamber were

considered to compute dental tissue volumes and metric mea-surements. Following Kupczik and Hublin (2010), the crown was separated virtually from the root based on the best-fit plane computed at the cervical line in Avizo. An additional plane parallel to the cervical plane was created, passing through the centre of the bifurcational zone (Fig. 2). Eight measurements were then collected from the root (Fig. 2; for more details see Kupczik and Hublin, 2010): 1) root length (from the cervical plane to the apex of the root); 2) total root volume (the volume of the root below the cervical plane, including dentine and pulp); 3) root stem volume (the volume of the root between the cervical plane and the plane at bifurcation); 4) root apex volume (the volume of the root below the plane at bifurcation); 5) pulp volume; 6) coronal pulp volume (portion of the pulp above the cervical plane); 7) root pulp volume (portion of the pulp below the cervical plane); and 8) cervical plane area (the section obtained by the cervical plane). Dental tissue volumes and metric measurements computed from the root and pulp chamber of San Bernardino 4 were compared with similar measurements gathered by Kupczik and Hublin (2010) from a sample of Neandertal, early *H. sapiens* and recent *H. sapiens* M3s.

Ancient DNA sequence processing

The root of San Bernardino 4 was drilled and about 24 mg of powder was sampled for DNA analysis. This bone powder was used to prepare 100 uL of DNA extract using the DNA extraction method described in Dabney et al. (2013). A single library was produced from 20 out of 100 ul of DNA extract using a double stranded library preparation method (Kircher et al., 2012) without enzymatic removal of deaminated cytosines. To prevent contamination from sequences derived from modern DNA libraries, the library adaptors carried project-specific barcodes. To retrieve complete mtDNA, we next used a protocol for targeted DNA sequence retrieval that is particularly suited for isolating mtDNA fragments (Maricic et al., 2010). The enriched libraries were sequenced from both ends on the Illumina GAII platform, using 76 cycles for each read. Fragments were included in further analyses if their forward and reverse reads overlapped by at least 11 base pairs (bp) and thus could be merged into single sequences. This removes all fragments over 141 bp from

analysis, but reduces errors at the 3′ ends of Illumina reads where error rates are at the highest. We aligned the sequences to the revised Cambridge Reference Sequence (rCRS) using an iterative mapping assembler, MIA. This alignment program is suited for aligning ancient DNA sequences because it takes into account the frequent sequence errors associated with base damage in ancient DNA sequences. The average unique coverage across the mtDNA of this library is 385.5-fold (Fig. S7). Based on ancient DNA sequence authenticity (see SOM for more details; Figs. S7 and S8), we concluded that the human DNA extracted from San Bernardino 4 comes from a single individual and that it is likely to be endogenous to this tooth.

AMS radiocarbon dating and isotope analyses

Extraction of collagen and isotopic measurements were performed at the laboratories of the Max Planck Institute for Evolutionary Anthropology using the method proposed by Talamo and Richards (2011; see SOM for more details).

The preservation of the bone collagen was established by measuring the C:N ratio, $\delta^{13}C$ and $\delta^{15}N$, %C and %N, and yield of the extract (Ambrose, 1990; Klinken, 1999), all of which fall within the acceptable range for collagen. The collagen was sent to the Klaus-Tschira-AMS facility of the Curt-Engelhorn Centre in Mannheim (Germany) for AMS radiocarbon dating (Kromer et al., 2013).

In addition, the results of the carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope analyses have allowed us to draw some conclusions on the diet of the San Bernardino 4 individual.

Results

Root morphology

The dental tissue volumes and root measurements of San Bernardino 4 and the comparative samples are reported in Table 1. The tooth in question has a large root volume, and the computed Z-score is closer to *H. neanderthalensis* than *H. sapiens*. For two other measurements (root length and cervical plane area), the results are ambiguous. The long root length finds correspondence with both
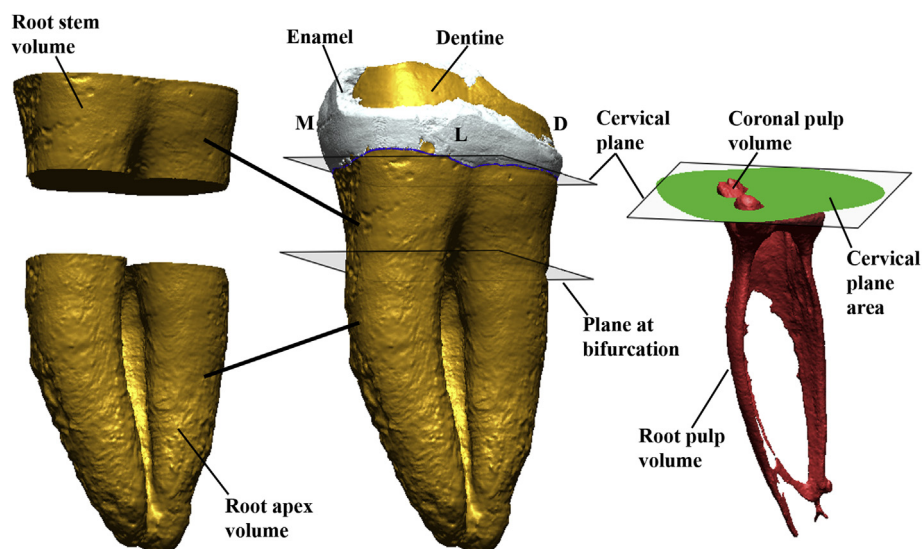
Figure 2. Basic steps involved in measuring the root of San Bernardino 4 LRM3: the root was separated from the crown based on the best-fit plane computed at the cervical line (cervical plane). An additional plane, parallel to the cervical plane and passing through the centre of the bifurcational zone was created (plane at bifurcation). Based on these two planes, the root and the pulp were separated in the following parts: root stem volume, root apex volume, coronal pulp volume and root pulp volume. The cervical plane also allows the identification of the cervical plane area.

early *H. sapiens* (e.g., the Aterians) and Neandertals, whereas its relatively small cervical plane area provides Z-scores close to both Neandertals and recent *H. sapiens*. Less ambiguous are the results obtained for the remaining five measurements, which align San Bernardino 4 with either the Aterian *H. sapiens* (for root apex volume and coronal pulp volume) or recent *H. sapiens* (for root stem volume, pulp volume and root pulp volume). Indeed, the specimen from San Bernardino has a small pulp chamber (not taurodontic), which finds parallels only among recent modern humans. Moreover, the bifurcation of the roots occurs more cervically, thus contributing to decrease the root stem volume, which is a typical trait of recent *H. sapiens* (Table 1). Overall, these results do not support the attribution of San Bernardino 4 to *H. neanderthalensis*, but they suggest its affiliation to either early *H. sapiens*, or more likely to recent modern humans.

Ancient DNA

We aligned the mtDNA sequence obtained from San Bernardino 4 to 54 present-day global modern human mtDNA sequences and one complete Neandertal mtDNA sequence. From the phylogenetic tree, it is clear that the mtDNA sequence we obtained is different from *H. neanderthalensis*, falling within the range of present-day *H. sapiens* variability (Fig. S9).

AMS radiocarbon dating

The isotopic results, C:N ratios and collagen yields for the dentine are well within the accepted ranges (Table 2). The date was corrected for a preparation background estimated from ^{14}C free bone samples, kindly provided by the ORAU (Oxford Radiocarbon Accelerator Unit) and pretreated in the same way as the archaeological sample. The radiocarbon date is 440 ± 21 ^{14}C BP and was calibrated using OxCal 4.1 (Bronk Ramsey, 2009) and IntCal09 (Reimer et al., 2009), (Fig. S10, Table 2). The LRM$_3$ belongs to a recent modern human dated to 1420−1480 cal AD (Cal 2 sigma), which corresponds to the end of the Middle Ages.

Carbon and nitrogen isotope analyses

The isotope composition of the dentinal collagen of San Bernardino 4 allows us to make some inferences about the diet of this individual during the formation of the tooth, according to principles reviewed by Lee-Thorp (2008) and summarized in the SOM. The third molars form between the ages of seven and 13 years, with the roots of the third molars being fully formed between 17 years and the early 20s (Hillson, 1996). Trophic level shifts linked to breastfeeding can, therefore, be discounted in the case of this specimen. The δ^{13}C ratio ($-17.8‰$) obtained from the tooth is elevated compared with values from humans living in

environments characterized by C$_3$ plant-dominated vegetation, such as those typical of pristine southern European terrestrial biomes (Mannino et al., 2012). This δ^{13}C value falls significantly outside the known range for Neandertals (Bocherens, 2009; Richards and Trinkaus, 2009) and is also higher than values obtained from the bone collagen of two late Upper Paleolithic *H. sapiens* from northeast Italy (Vercellotti et al., 2008; Gazzoni et al., 2013), as well as of most prehistoric hunter-gatherers analyzed from the Mediterranean region (as reviewed by Mannino et al., 2012: Table 1). On the other hand, the δ^{13}C value from San Bernardino 4 is lower than the values recorded from the bone collagen of the Bronze Age humans from Olmo di Nogara (Tafuri et al., 2009). These individuals consumed relatively high proportions of protein from C$_4$ plants, such as millet, which was introduced to northeast Italy sometime between the Neolithic and the early Bronze Age.

The δ^{15}N value (10.3‰) falls within the range for prehistoric and historic humans with largely terrestrial diets, including Neandertals (Bocherens, 2009; Richards and Trinkaus, 2009). However, nitrogen isotope composition of bone collagen varies not only with trophic level, but also through time and space due to changes in temperature and aridity (Richards and Hedges, 2003; Hedges et al., 2004). Without δ^{15}N values of associated and contemporary fauna from the site, we cannot conclude more about the diet using the nitrogen isotope ratio alone.

Overall, the humans analyzed from southern Europe with the most similar carbon and nitrogen isotope compositions to San Bernardino 4 belong to Medieval age groups, whose diet was centred on foods from terrestrial ecosystems, but probably included millet, which, as mentioned above, was introduced to this region no earlier than the Middle Holocene (Reitsema and Vercellotti, 2012; Ciaffi et al., 2013).

Discussion and conclusions

The morphometric analysis of the San Bernardino 4 LM$_3$ root and the ancient DNA do not support the attribution of the specimen to *H. neanderthalensis*, but rather to *H. sapiens*. Moreover, direct ^{14}C dating of the tooth provided a recent age, close to the end of the Middle Ages (1420−1480 cal AD, 2 sigma), which is obviously inconsistent with the Mousterian layers in which the tooth was discovered. The dietary inferences based on the isotope analyses also suggest that this individual was not a Neandertal. The LM$_3$ must, therefore, be considered an intrusive recent *H. sapiens* specimen that found its way into the Mousterian macro-unit II as a result of post-depositional disturbance during Medieval or post-Medieval times (for example, during the building of the wall at the entrance of the cave; see SOM). In light of the results obtained on the LM$_3$, even though we do not have ancient DNA data and direct ^{14}C dates for the San Bernardino 3 distal phalanx and the San

Table 1
Dental tissue volumes and root metrics of San Bernardino 4, Neandertals, early and recent *Homo sapiens*.[a]

Measurements	S. Bernardino 4	Neandertals			Early *H. sapiens* (Aterians)			Recent *H. sapiens*		
		n	Mean (SD)	Z-score	n	Mean (SD)	Z-score	n	Mean (SD)	Z-score
Root length (mm)	16.45	15	16.34 (2.05)	**0.05**	3	16.42 (1.66)	**0.02**	20	12.85 (2.03)	1.77
Root volume (mm^3)	646.03	15	757.26 (168.99)	**−0.66**	3	722.78 (31.21)	−2.46	20	375.23 (109.31)	2.48
Root stem volume (mm^3)	284.82	14	670.05 (251.47)	−1.53	3	410.05 (18.69)	−6.70	8	251.96 (50.85)	**0.65**
Root apex volume (mm^3)	361.22	14	96.09 (107.89)	2.46	3	312.73 (47.19)	**1.03**	8	128.06 (137.93)	1.69
Pulp volume (mm^3)	28.11	14	69.03 (25.40)	−1.61	3	66.97 (36.51)	−1.06	9	33.30 (13.72)	**−0.38**
Coronal pulp volume (mm^3)	1.04	13	10.07 (5.93)	−1.52	3	7.31 (11.20)	**−0.56**	8	5.96 (2.55)	−1.93
Root pulp volume (mm^3)	27.07	13	60.78 (23.08)	−1.46	3	59.68 (26.55)	−1.23	8	28.19 (15.19)	**−0.07**
Cervical plane area (mm^2)	78.04	14	82.68 (8.54)	**−0.54**	3	97.23 (13.09)	−1.47	20	71.12 (12.09)	**0.57**

Low Z-scores in bold.
[a] Comparative data from Kupczik and Hublin (2010).

Table 2
Results of carbon and nitrogen isotope analyses, C:N ratios and collagen yields for San Bernardino 4.

Code	MPI Lab Nr.	%Coll	$\delta^{13}C$	$\delta^{15}N$	%C	%N	C:N	AMS Nr.	^{14}C age	Err 1σ	Cal 1 sigma	Cal 2 sigma
SP3006	S-EVA 27007	13.54	−17.85	10.29	45.93	17.13	3.13	MAMS-17739	440	21	1430−1460 cal AD	1420−1480 cal AD

$\delta^{13}C$ values are reported relative to the vPDB standard and $\delta^{15}N$ values are reported relative to the AIR standard. Radiocarbon result obtained from Mannheim AMS, Calibrated using OxCal 4.1 (Bronk Ramsey, 2009) and IntaCal 09 (Reimer et al., 2009) calibration curve.

Bernardino 5 Rdi$_2$, the small size and morphology of both specimens compared with Neandertals and Upper Paleolithic *H. sapiens* (Tables S2 and S3) strongly suggests that they also belong to recent *H. sapiens*, post-depositionally introduced in the Mousterian deposits during historic times.

Based on these results, the human remains from macro-unit II of San Bernardino Cave must be removed from the Catalogue of Italian Fossil Human Remains (Alciati et al., 2005), and not considered in future comparative studies of fossil hominins for morphological or morphometric analyses.

As a final remark, the case of San Bernardino provides a good example of the need to reassess the taxonomy of human remains discovered and studied decades ago (see also Benazzi et al., 2011b). Due to methodological limitations, the taxonomic discrimination of Late Pleistocene human remains has often been influenced by the archaeological context in which the fossils were discovered, and on the assumption that, at least in Europe, Neandertals were the makers of Mousterian technocomplexes. Like San Bernardino, other human fossils might require thorough investigations either to confirm their taxonomic status or because they are unknown to the scientific community. This is particularly true for small remains such as isolated teeth. For example, the M$_3$ Hunas 1 (Germany), recovered in a Mousterian layer and originally attributed to a Neandertal by Alt et al. (2006), has been reclassified as a recent *H. sapiens* and deemed to be intrusive on the basis of the morphometric analysis of the root (Kupczik and Hublin, 2010). Moreover, sometimes the available information is so scarce, such as for the Leuca I M^2 recovered in 1958 at Grotta del Bambino near Santa Maria di Leuca (Apulia, Italy), that a complete morphological description and detailed comparative morphometric analysis was needed before the specimen could be used in comparative analysis (Benazzi et al., 2013).

In this contribution we have shown that improved methods for dental morphometric analysis, ancient DNA, ^{14}C dating, and isotope analyses can be combined to support or refute previous taxonomic assessments. Although it is essential to discover new fossils, we emphasize that it is equally important to validate the antiquity and taxonomic attributions of specimens found and studied in the past, because erroneous attributions are likely to affect our understanding of human evolution.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jhevol.2013.09.009.

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