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Are there marrow cavities in Pleistocene elephant limb bones, and was marrow available to early humans? New CT scan results from the site of Castel di Guido (Italy)

Abstract

CT-scan analyses were carried out on limb bones of straight-tusked elephants (*Palaeoloxodon antiquus*) from the Middle Pleistocene site of Castel di Guido (Italy), where bifaces made of elephant bone were found in association with lithics and a large number of intentionally modified bone remains of elephants and other taxa. CT-scans show that marrow cavities are present within the limb bones of this taxon. Though rather small compared to the size of the bones, these cavities suggest that bone raw material procurement may not have been the unique goal of intentional elephant bone fracturing, and the marrow may also have been extracted for consumption.

Keywords

Pleistocene; Italy; *Palaeoloxodon antiquus*; limb bones; CT-scan; marrow cavities; Lower Palaeolithic; marrow consumption

1. Introduction

When the dietary preference of the genus *Homo* shifted to meat and fat some 2 million years ago (Potts and Shipman, 1981; Milton, 1987; Speth, 1989; Aiello and Wheeler, 1995; Domínguez-Rodrigo and Pickering, 2017; Thompson et al., 2019), Proboscideans became a preferred food resource among humans (Ben-Dor et al., 2011; Agam and Barkai, 2018). The exploitation of elephant/mammoth/stegodon carcasses is documented in many Lower, Middle and Upper Pleistocene single- or multiple-carcass sites in Europe (Gaudzinski and Turner, 1999; Mania and Mania, 2005; Boschian and Saccà, 2010; Anzidei et al., 2011; Saccà, 2012a; Yravedra et al., 2010; 2012; 2014; Panera et al., 2014; Konidaris et al., 2018), Africa (Klein, 1988; Echassoux, 2012; Domínguez-Rodrigo et al., 2014; Yravedra et al, 2017), Western (Goren-Inbar et al., 1994; Rabinovich et al., 2012) and Eastern Asia (Yuan et al., 2012; Zhang et al., 2010), but also in the Upper Pleistocene (Holen, 2006; 2007; Holen and May, 2002) and possibly in the Middle Pleistocene of North America (Holen et al., 2017).

The consumption of elephant meat and fat has been definitively demonstrated at several sites by the occurrence of clear though necessarily infrequent cut marks (Crader, 1983; Haynes, 1991, pp. 185-186; Yravedra et al., 2010) that indicate defleshing and butchery (Wenban-Smith et al., 2006; Yravedra et al., 2010; Boschian and Saccà, 2010; 2015; Saccà, 2012a; Rabinovich et al., 2012). The exploited part of the carcass also included post-cranial elements (limbs, internal organs, and subcutaneous fat) as well as the soft parts of the head (e.g., the brain, tongue, or fat deposits in the temporal gland; see Goren-Inbar et al., 1994; Agam and Barkai, 2016). More specifically, cut marks appear on scapulas and ribs of elephants at the Lower Palaeolithic Revadim site in Israel as well as at Castel di Guido in Italy, indicating filleting of meat and probably intentional access to the internal organs (Rabinovich et al., 2012; Saccà, 2012a). Residues of fat as well as use-wear marks were detected on a biface and a scraper associated with butchered animal remains, including an elephant rib bearing cut marks (Solodenko et al., 2015).

After being stripped of meat and fat, elephant bones were also the source of marrow exploited for consumption, and bone fragments were exploited to fashion tools. In particular regions, mainly in tree-free tundra landscapes, mammoth bones were also exploited as an essential source of raw material for building dwellings (e.g. Iakovleva, 2015) and as fuel (e.g. Bosch et al., 2012).

Marrow is thought to have played an important role in satisfying the dietary needs (Speth and Spielmann, 1983; Thompson et al., 2019) and preferences of the foragers. Bone fat (marrow) is superior (greater percentage of fatty acids/chemical fat) to the fat found in the rest of an animal carcass (Brink, 1997; Outram and Rowley-Conwy, 1998). However, elephant marrow exploitation by humans has been questioned either because of scant evidence (Villa et al., 2005), or because the elephant limb bones were thought to have lacked yellow marrow cavities and been entirely filled by cancellous bone tissue (Shoshani, 1996: p. 9; Fowler and Mikota, 2008: p. 272), which would have made direct and easy extraction of this important dietary resource difficult if not impossible, unless specific techniques were used. However, the extensive and systematic fracturing of fresh limb bones (as demonstrated by the spiral fracturing pattern) at Castel di Guido (Boschian and Saccà, 2010; 2015; Saccà, 2012a) and at the PRERESA site in Spain (Yravedra et al., 2012: p. 1068) strongly suggest that elephant bone marrow was in fact actively extracted. It should be noted however, that the excavators of the PRERESA site found this evidence difficult to comprehend since, in their view, “elephant bones lack the medullary cavity and instead have perforated bone tissue” (Yravedra et al., 2012: p. 1064), and thus the subject of the extractability of elephant bone marrow is still a cause of confusion. We believe, however, that the archaeological evidence is consistent with the purposeful breakage of elephant limb bones, and that the most parsimonious explanation for such a behavioural pattern is the extraction of marrow. In this paper we provide evidence that reinforces such a hypothesis.

The use of elephant bone for making tools – mostly bifaces – is well documented at several Palaeolithic sites in Europe (Cassoli et al., 1982; Segre and Ascenzi, 1984; Radmilli and Boschian, 1996; Anzidei, 2001;

Dobosi, 2001; Gaudzinski et al., 2005; Boschian and Saccà, 2010; 2015; Saccà, 2012b), in the Levant (Rabinovich et al., 2012), in Africa (Leakey, 1971; Backwell and D'Errico, 2004; Echassoux, 2012; Beyene et al., 2013) and in China (Wei, 2017). Proboscidean bones were also used for the production of tools other than bifaces, also in North America (Johnson, 2001; Holen, 2006; 2007; Holen and May, 2002). The reasons for using this particular material in biface production are not fully clear. The standard hypothesis is that the shortage of high-quality stone was the reason for the use of bone in biface production; however, this hypothesis has never been rigorously tested. Other hypotheses have also been proposed, in the spirit of the arguments suggested in Tanner (2014), focusing on ontological and cosmological conceptions expressed in human-proboscidean interactions, which led to the production of bifaces from elephant bones (Zutovski and Barkai, 2016, Barkai, 2019).

The extraction of marrow for consumption and the use of bone fragments for tool shaping both require the thorough fracturing of large and thick bones, regardless whether the two purposes are concurrent or not. Marrow extraction requires reasonably early access to the inside of the bones and consequently produces "green bone" fracturing, whereas bone knapping is better performed on somewhat drier – even if not completely dry – bone (Backwell and D'Errico, 2004) and produces very similar or indistinguishable fractures. The use of bone in shaping bifaces is less straightforward than breaking bone for marrow extraction, as it may have involved distinct stages: unexploited bones may have been left behind after meat and fat stripping, to be opened later for marrow extraction. The resulting bone chunks and slabs may have been used as "blanks" for tool knapping, generating an intricate assemblage of fracturing patterns. It may consequently be difficult to ascertain the reason (or reasons) why elephant bones were broken (for marrow extraction or tool fashioning, or both), if no other clues are collected from the bone assemblage.

The production of expedient bone tools may have been fostered more or less casually by the large number of bone slabs available after breaking elephant bones for marrow extraction, because the shape of some of these bone fragments might often be evocative of typical handaxe morphology. Conversely, more complex cognitive processes would have been involved in the intentional extraction of suitable materials from nutritionally irrelevant bones.

It should also be emphasized that an accurate cost/benefit evaluation is crucial to the interpretation of these contexts: breaking elephant bones is not an easy task, given the size and weight of the hammerstones needed for efficiently fracturing fresh bones of modern elephants, as demonstrated experimentally (Holen et al., 2017: pp. 484-485, 495), and given that *Palaeoloxodon antiquus* bones are much thicker and tougher than those of extant elephants.

These results make it clear that verifying whether medullary cavities – and easily accessible marrow –really do exist in elephant limb bones is crucial to the interpretation of cultural sites where this taxon is an important component of the faunal assemblage. If cavities exist and yielded a reasonable quantity of marrow at an acceptable energetic cost/nutritional benefits ratio, it is possible that these bones may have been purposely opened to extract marrow. This hypothesis is likely for any site with evidence of proboscidean carcass exploitation, regardless of the occurrence of bone industry (even if its absence is not proof that bone was not exploited in tool production). Conversely, there is some uncertainty in interpreting archaeological contexts whose tool assemblages include bone industry, because it is difficult to ascertain whether bones were processed with the twofold goal of procuring material for tool shaping and extracting marrow, or only for producing tools.

We aim to shed light on this question by determining whether yellow marrow cavities are present in Pleistocene elephant limb bones, and if so, by determining their location and size. To this end, we examine the inner structure of some unfragmented or very partially fragmented *Palaeoloxodon antiquus* limb bones excavated at the late Middle Pleistocene (MIS 9) Lower Palaeolithic site of Castel di Guido (Italy). The association of an extensive assemblage of thoroughly fractured bones with a large set of bone bifaces and stone industry makes this site the ideal place to inquire about the connections between food procurement, toolmaking, and the anatomical characteristics of *Palaeoloxodon antiquus*.

2. The site

Castel di Guido (Radmilli and Boschian, 1996, Boschian and Saccà, 2010; 2015; Saccà, 2012a) (Fig. 1) is a 327-260 ka old Middle Pleistocene site (Michel et al., 2001; Michel et al., 2009), although more recent dates obtained from other sequences of the area may suggest a MIS 11 age of around 412±2 ka (Marra et al., 2018). Bones found at the site include those of elephants (*Palaeoloxodon antiquus*), aurochs (*Bos primigenius*), horses (*Equus ferus*) and a few other mammals. The bones, almost all of which were fragmented, were found together with an industry including large biface-like artefacts made of stone and elephant bone (Fig. 2) and small-size tools made of flint pebbles and flakes, and choppers and chopping tools (Radmilli and Boschian, 1996; Saccà, 2012b; Villa et al., 2016). Numerous Middle Pleistocene sites bearing elephant remains, lithic industries, and bones shaped in different manners can be found in the region around Rome, e.g., Torrimpietra (Damiani et al., 1988; Blanc, 1954; Malatesta, 1978a; Malatesta, 1978b, Villa et al., 2016), La Polledrara di Cecanibbio (Anzidei et al., 1989; Anzidei and Arnoldus-Huyzendveld, 1992; Anzidei and Cerilli, 2001; Anzidei et al., 2012, Santucci et al. 2016), Malagrotta (Cassoli et al., 1982), Rebibbia-Casal de' Pazzi (Anzidei and Ruffo, 1985; Anzidei, 2001), and Fontana Ranuccio (Segre and Ascenzi, 1984; Segre et al., 1987). It is unclear whether the concurrence of such unique sites in a limited area was due to cultural, environmental, or taphonomic reasons.

At the site of Castel di Guido, the numerous shaped bone tools are associated with a large number of highly fragmented animal bones. Among these, the dominance of nutritionally relevant bones – i.e. those including medullary cavities – suggests intensive marrow extraction and expedient bone tool fashioning. Conversely, skeletal elements including no or very little potential marrow (tusks, scapulae, ribs, etc.) were rarely fractured (Saccà, 2012a; 2012b).

The abundance of bone artefacts is the most outstanding characteristic of this site and is unparalleled elsewhere. Tools that can be identified as bifaces or biface-like are particularly numerous within the bone industry and occur also within the stone tool assemblage (9% of the shaped stone items). The bone industry at Castel di Guido is of relatively high technological quality in comparison to other Late Middle Pleistocene sites of the area: there is a whole range of artefacts more or less intensely modified by flaking.

These artefacts range from bone slabs with a couple of detachment scars that can hardly be considered as intentional, to typical bifaces shaped by more than one generation of detachments (Saccà 2012b). However, the tools that can be indisputably classified as bifaces are relatively few.

At the other sites, bone artefacts are generally much less frequent, and the indisputable bifaces or biface-like tools may be entirely lacking, as at La Polledrara (Anzidei, 2001), or may include only one or a few items, as at Malagrotta (Cassoli et al., 1982) or Fontana Ranuccio (Segre and Ascenzi, 1984; Segre et al., 1987).

Almost all the remains found at Castel di Guido lie flat in a single level on the bottom of a former gully and are organised in a complex palimpsest of probably several human occupations separated by phases of river erosion/reworking. Despite frequent *ab antiquo* reworking, the distribution of the remains indicates that some areas can still be used to assess site use. Some bone clusters are organised similarly to their original position within the carcass and are *in situ*, suggesting that elephant carcasses were processed by humans on site, and probably also in nearby areas where they were not preserved because of successive landscape modelling. Some of the remains were subsequently reworked during flow reactivation phases, while others derive from inputs external to the gully (Boschian and Saccà, 2010; Saccà 2012a).

All these data point to a long but discontinuous period of site use, characterised by several phases of use/frequentation, variably spaced in time.

3. Materials and methods

A small cluster of twelve (Tab. 1) unprocessed *Palaeoloxodon antiquus* limb bones was found in 1989 during summer fieldwork at Castel di Guido. These bones represent an exception within the bone assemblage at the site, because they are unfragmented or moderately fragmented *in situ* by taphonomic agents; only a few of them are incomplete and no traces of modification by humans (fracturing, cut marks, etc.) were observed. These remains were not lying on the bottom of the gully, in contrast to all the other remains, but were chaotically embedded in the overlying sediment at a height between 20 and 110 cm from the bottom. This sediment testifies to a medium-energy lacustrine environment or a *lahar*, with an age close to that of the bone assemblage (V. Michel, personal communication; Marra et al., 2018). The minimum number of individuals indicated by these remains is three elephants, with largely incomplete individuals that probably represent the accumulation of parts of carcasses or of isolated bones when the gully eventually filled up.

These bones had been stored in a Castel di Guido local facility, and only the few better preserved (n = 5) items (Tab. 2, Fig. 3) were chosen to be transported to the laboratory in Pisa and analysed by medical CT scanning (Fig.4). The others were observed in situ and partial measurements were taken when possible.

CT images were acquired by a GE Medical System LightSpeed RT 16 clinical scanner. Acquisition parameters were the following: data collection diameter 500 mm; matrix 512x512; slice thickness 1.25 mm; slice spacing 1.25; X-ray tube current 320 mA; X-ray tube tension 120 kV.

The CT scan data were imaged by Avizo 6.3.1 3D Visualization Software for Scientific and Industrial Data, by Visualization Sciences Group, SAS, and examined by transverse and longitudinal sectioning in relevant loci of the bones. Segmentation was carried out in order to separate compact tissue, cancellous tissue, and internal voids. Eventually, internal voids, cancellous tissue, and compact tissue were 3D-modelled after segmentation to estimate their volume.

4. Results

The CT scanning of this small (n = 5) *Palaeoloxodon antiquus* bone assemblage shows that only some of the examined bones include medullary cavities, which in most cases are rather small; measures are reported in Table 3. The largest cavities occur in femura CdG29 (Fig. 5) and CdG30 (Fig. 6), always representing less than 1% of the total bone volume. Very small cavities occur in the humerus CdG36 (Fig. 7) and in one subadult/adult tibia (CdG26, Fig. 8), whereas the tibia of a young individual (CdG43, Fig. 9) is completely filled with cancellous tissue.

Macroscopic observations carried out on breakage surfaces of other bones that could not be transported outside the storage facility are consistent with the CT-scan results (CdG32, Fig. 10, and CdG06, Fig. 11). Medullary cavities of the same size as those observed under CT-scanning occur at mid-shaft in femur CdG06, whose fully fused epiphyses indicate an age of >30 years. Cavities are not present in the metaphyses of an unscanned femur (CdG32) whose partially fused proximal epiphysis suggests an approximate age of <29 years. An ulna (CdG19) with an unfused distal epiphysis (>24-32 years, but possibly older) is also completely filled with cancellous tissue at mid-shaft (age estimates following C. Craig, unpublished data cited in Haynes, 1991: Table A15, Appendix p. 351).

The volume of the cancellous tissue, compared to the total bone volume (Tab. 4), is generally larger in the younger individuals. The voids among the trabeculae of the diaphyseal cancellous bone are rather wide, up to 5 mm, mostly in the older individuals, whereas the porosity is finer (1–2 mm) within the epiphyses.

5. Discussion

The results of this work show, for the first time in Middle Pleistocene specimens, that marrow cavities do occur within some limb bones of adult individuals of *Palaeoloxodon antiquus* from Castel di Guido. However, interpreting the evidence provided by these data is not easy, mostly because of the small size of the sample. In the femur, the medullary cavities are rather small compared to the size of the bone. Here, the quantity of directly extractable marrow compared to the total bone size is much less than in modern *Loxodonta africana*. The difference is evident in Holen et al. (2017: Extended Data Fig. 8c), where globs and lumps of fat yellow marrow spontaneously drop out of the large medullary cavity of a fractured bone. At least in some individuals of *Elephas maximus* taxon, bones do not include marrow cavities (Nganvongpanit et al., 2016). At Castel di Guido, only smaller cavities were observed within the humerus and tibiae, particularly of the older individuals.

The data from our study is insufficient to show any definite correlation between medullary cavity size and elephant age.

As mentioned above, modern experiments in fracturing a limb bone of a modern *Loxodonta africana* (Holen et al., 2017: Extended Data Fig. 8c) put into light a significant quantity of marrow included within a wide medullary cavity. Similar evidence can be viewed in a scene from a documentary film that shows a pygmy group from the Congo rainforest butchering a hunted elephant (Duffy, K., Pygmies of the Rain Forest; the film can be viewed at https://archive.org/details/pygmiesoftherainforest). After a group of males has stripped the elephant carcass of meat and fat, a pygmy male cracks open one of the elephant limb bones using an axe (the specific scene can be viewed at 24:08–24:30) and significant quantities of marrow are extracted by hand and eaten by children.

However, at this stage of research we are archaeologically unable to bridge the gap between the significant quantities of marrow documented in the modern experiment and in the documentary film, versus the much smaller quantities indicated by the CT scans of the Pleistocene elephant limb bones from Castel di Guido. These cavities are associated with archaeological evidence of extensive bone fracturing, clearly indicating extraction of marrow, however small in quantity. Moreover, previous studies at the Castel di Guido site indicated that early humans made use of all parts of the elephant (Boschian and Saccà, 2015); thus, it goes without saying that the highly nutritious bone marrow was extracted as well. We hope that further studies will shed light on this discrepancy.

It is difficult to evaluate whether the small volume of available yellow marrow justified the high energy consumption needed for fracturing all the extremely robust elephant limb bone diaphyses, whose compact bone can be up to 6 cm thick. However, the fractured bones unearthed at several Middle Pleistocene sites provide solid evidence regarding the actual practice of bone marrow extraction by early humans. Compared to the intensive exploitation of much smaller amounts of marrow included in bones of smaller taxa observed in other forager contexts, this very small amount probably did justify fracturing bones for yellow marrow consumption. Despite the small size of the medullary cavities, the elephant bones may have been appealing for nutritional purposes because the high porosity of the diaphyseal trabecular bone may have facilitated the further extraction of larger quantities of grease. This hypothesis is corroborated by the common occurrence of fractured bones whose compact tissue is too thin to be suitable for tool fashioning.

A recent study has shown the significant caloric contribution of Pleistocene proboscideans to human nutrition, based on the analysis of frozen mammoths found in the permafrost of Siberia (Guil-Guerrero et al., 2018). Following the significant content of essential fatty acids in Pleistocene mammoths, the authors argue that fat-rich organs were essential for survival, as they provided much more energy than meat, and thus "brain, bone marrow, subcutaneous fat, viscera and meat would have been the targeted mammoth organs for Stone Age hunters" and "given the high energy needs of Stone Age hunters, protein-rich food, such as meat, should have been ingested to a lower extent than other fatty tissues" (Guil-Guerrero et al. 2018:459). According to this study, "Achieving 4500 kcal, the previously estimated daily energy need at those times, would have been possible by consuming ∼566 g of meat complemented by ∼592 g of fatty tissues, such as subcutaneous fat. For a mammoth of ∼3.0 tons, ∼5% subcutaneous fat and other similar fats distributed throughout the body would be a conservative figure, and thus a medium-sized mammoth would have stored ∼1 million kcal as fat, providing clean energy for a hunting group of 12–24 individuals for approximately 9–18 days, while the consumption of variable amounts of meat would have extended this figure for some days" (Guil-Guerrero et al., 2018:461). This study provides vivid evidence of the central role of proboscideans in human adaptation during Palaeolithic times; however, even these estimations do not take into account the contribution of bone marrow. Thus, when bone marrow is added to the calories and fatty acids obtained from elephant fat and meat, the dietary potential of proboscideans is even further emphasised. On the other hand, the availability of good quality raw material represented by the thick compact tissue of some bones should have been appealing for technological purposes and may have represented a value-added by-product that was worth the fracturing effort, despite the relatively modest quantity of nutritious substance.

6. Conclusions

These new data indicate that the exploitation of elephant limb bones for exclusive marrow extraction may have been possible and cost-effective in terms of obtained food versus energy expended in fracturing. This hypothesis can explain the occurrence of thoroughly fractured bones in contexts where no bone tools were fashioned from elephant bone raw material. It is difficult to explain why Middle Pleistocene humans painstakingly extracted a quantity of marrow that was some orders of magnitude less than the mass of meat and fat available in the elephant carcass. However, it can be hypothesised that the exploitation of the carcass lasted for a long time and that marrow extraction was deferred to later phases/seasons of much poorer food availability, well after all the meat had been stripped from the carcass. On the other hand, as seen in the Congo example, marrow could have been extracted in the course of carcass manipulation and might have had special significance in terms of taste or nutritional qualities (Reshef and Barkai, 2015). In fact, we do not know how long edible marrow can be preserved within unfractured bones; this depends also on physiological, digestive and cultural characteristics of Palaeolithic humans (see, for example, Speth, 2017 for an argument regarding the plausibility of the consumption of putrid meat in Palaeolithic times).

The technological peculiarities of elephant bone can explain why these bones were fractured, but the contextual availability of marrow explains why the unmodified bone fragments largely outnumber the tools in sites like Castel di Guido.

Considering the small sample of bone examined here, a more accurate study on the structure of a statistically reliable number of extant and extinct proboscidean limb bones should be carried out, taking into consideration also the age of the individuals examined. Whatever the results of this future study, the data presented here suggest an additional possible use of elephant carcasses for consumption, showing that marrow was available within at least some of the proboscidean bones available to Palaeolithic human groups.

Tables

NI	Anatomical ID	Portion preserved	Notes
CdG07	left humerus	proximal epiphysis	
CdG08	left humerus	distal epiphysis	
CdG36	left humerus	distal half	
CdG28	right humerus	distal epiphysis	
CdG19	right ulna	complete	broken (2 pieces)
CdG26	left tibia	almost complete	
CdG43	right tibia	proximal half	unfused (absent) epiphysis
CdG29	left femur	complete	
CdG30	right femur	almost complete	unfused (absent) *caput ossis femoris*
CdG32	left femur	complete	broken (4 pieces), fragmented proximal epiphysis
CdG06	right femur	complete	broken (4 pieces)
CdG33	femur	distal epiphysis	fragment

Table 1. Full set of unprocessed *Palaeoloxodon antiquus* limb bones from Castel di Guido.

NI	Anatomical ID	Age (years)		Measures (cm)				
				Bp	Bd	GL	GLC	SD
CdG43	right tibia	<18-24	juv					
CdG26	left tibia	>18-24		30.0	21.0	82.8		13.6
CdG36	left humerus	>18-19			37.5			16.0
CdG29	left femur	>30 (25-32)		44.0	31.5	128.5	133.0	18.8
CdG30	right femur	<30 (32)			28.0	131.0		20.0

Table 2. CT-scanned *Palaeoloxodon antiquus* bones. Age estimates following C. Craig, unpublished data cited in Haynes (1991: Table A15, Appendix p. 351), referred to extant African elephants. Measures following Von den Driesch (1976).

	Medullary cavity size (cm)		Volumes (cm^3)			
Bone ID	Width	Length	Marrow cavity	Spongy tissue	Compact tissue	Whole bone
CdG43	-	-	-	2632	1003	3634
CdG26	1.5	6.0	114	8893	7018	16026
CdG36	3.5-4.5	13.5 (26.2)	78	12978	13603	26660
CdG29	2.5 - 3.7	17.9	306	12280	25309	37895
CdG30	1.8 - 5.5	34.5	358	19370	18412	38139

Table 3. Distinct bone tissue and medullary cavity size and volumes. Measures of CdG43 and CdG36 refer respectively to the proximal and distal half of bones broken mid-diaphysis; CdG43 belongs to a juvenile individual and lacks the proximal epiphysis. The proximal epiphysis is also incomplete in CdG30.

Bone ID	Marrow	Spongy	Compact	Age (years)
CdG43	-	72.4	27.6	juv (<18-24)
CdG26	0.7	55.5	43.8	>18-24
CdG36	0.3	48.7	51.0	>18-19
CdG29	0.8	32.4	66.8	>30 (25-32)
CdG30	0.9	50.8	48.3	<30 (32)

Table 4. Volume percentage of medullary cavities, cancellous and compact bone tissues versus total bone volume and estimated individual age.

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Figure captions

Figure 1. Location map. Elevations (above sea level) 1: 0–100 m; 2: 100–200 m; 3: 200–300 m; 4: 300–500 m; 5: calderas; 6: rivers; 7: coastline. Solid circle: Castel di Guido.

Figure 2. Bifaces from Castel di Guido. A: stone tools; B: bone tools. Scale bar: 5 cm.

Figure 3. Photographs of the CT-scanned Castel di Guido *Palaeoloxodon antiquus* limb bones. CdG29: left femur caudal view; CdG30: right femur, caudal view; CdG26: left tibia, cranial, caudal, lateral and medial views; CdG43: right tibia, caudal, cranial, medial and lateral views; CdG36: left humerus, caudal and cranial views. Due to working space availability, the picture of CdG30 was obtained by stitching together six separate images and is slightly distorted distally. Scale bar: 25 cm.

Figure 4. Femur CdG29 during CT-scanning at Dipartimento di Ricerca Traslazionale e delle Nuove Tecnologie in Medicina e Chirurgia, Università di Pisa.

Figure 5. Left femur (CdG29) of >30 years old *Palaeoloxodon antiquus*, with completely fused epiphyses. Top: anterior/cranial view; bottom: lateral/left view. From left to right: CT-scan isosurface of the bone; orthoslice along transversal plane, showing the medullary cavity and the *canalis nutricius*; Segmentation of the trabecular (green) and compact (grey) tissue; segmentation of the medullary cavity (red). Red lines on isosurfaces indicate the traces of the orthoslices represented in the other views. Scale bar: 20 cm.

Figure 6. Right femur (CdG30) of <30 years old *Palaeoloxodon antiquus*, with unfused proximal epiphysis and missing *caput ossis femoris*. Top: anterior/cranial view; bottom: median/left view. From left to right: CT-scan isosurface of the bone; orthoslice along transversal plane, showing medullary cavity, *canalis nutricius* and several postdepositional (weathering) cracks; segmentation of the trabecular (green) and

compact (grey) tissue; segmentation of the medullary cavity (red). Red lines on isosurfaces indicate the traces of the orthoslices represented in the other views. Scale bar: 20 cm.

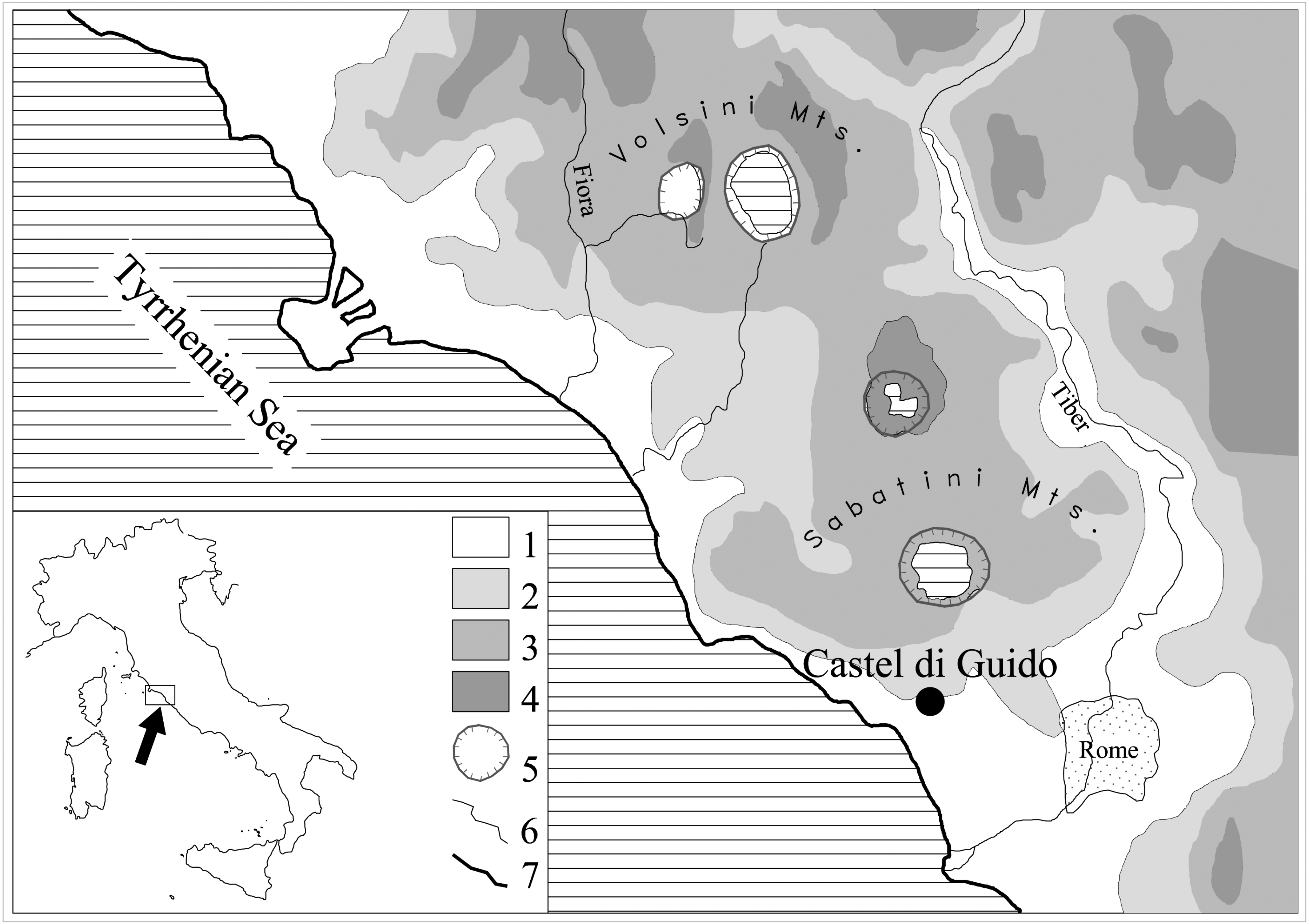
Figure 7. Distal part of left humerus (CdG36) of >18-19 years old *Palaeoloxodon antiquus*, with completely fused distal epiphysis. Top: anterior/cranial view; bottom: lateral/left view. From left to right: CT-scan isosurface of the bone; orthoslice along transversal plane; segmentation of the trabecular (green) and compact (grey) tissue; segmentation of the medullary cavity (red). Red lines on isosurfaces indicate the traces of the orthoslices represented in the other views. Scale bar: 20 cm.

Figure 8. Left tibia (CdG26) of >18-24 years old *Palaeoloxodon antiquus*, with completely fused epiphyses. Top: anterior/cranial view; bottom: lateral/left view. From left to right: CT-scan isosurface of the bone; orthoslice along transversal plane; segmentation of the trabecular (green) and compact (grey) tissue; segmentation of the medullary cavity (red). Red lines on isosurfaces indicate the traces of the orthoslices represented in the other views. Scale bar: 20 cm.

Figure 9. Proximal half of right tibia (CdG43) of <18-24 years old *Palaeoloxodon antiquus*, with unfused and missing proximal epiphysis . Top: anterior/cranial view; bottom: median/left view. From left to right: CT-scan isosurface of the bone; orthoslice along transversal plane; segmentation of the trabecular (green) and compact (grey) tissue. No medullary cavity. Red lines on isosurfaces indicate the traces of the orthoslices represented in the other views. Scale bar: 20 cm.

Figure 10. Left femur (CdG32), broken in several pieces, not CT-scanned. A: general view of the specimen in the storeroom of Comune di Roma Azienda agricola biologica "Castel di Guido". Note part of CdG29 in the bottom left corner. B, C: fresh post-excavation transverse fracture surfaces through the distal metaphysis, showing cancellous bone with large voids; D: bone shaft.

Figure 11. Right femur CdG06 of >30 years old *Palaeoloxodon antiquus*, with completely fused epiphyses, broken in several pieces, not CT-scanned. A: general view in the storeroom of Comune di Roma Azienda agricola biologica "Castel di Guido". B: taphonomic transversal stepped fracture through the central part of the diaphysis, showing wide medullary cavity and coarse-void cancellous bone.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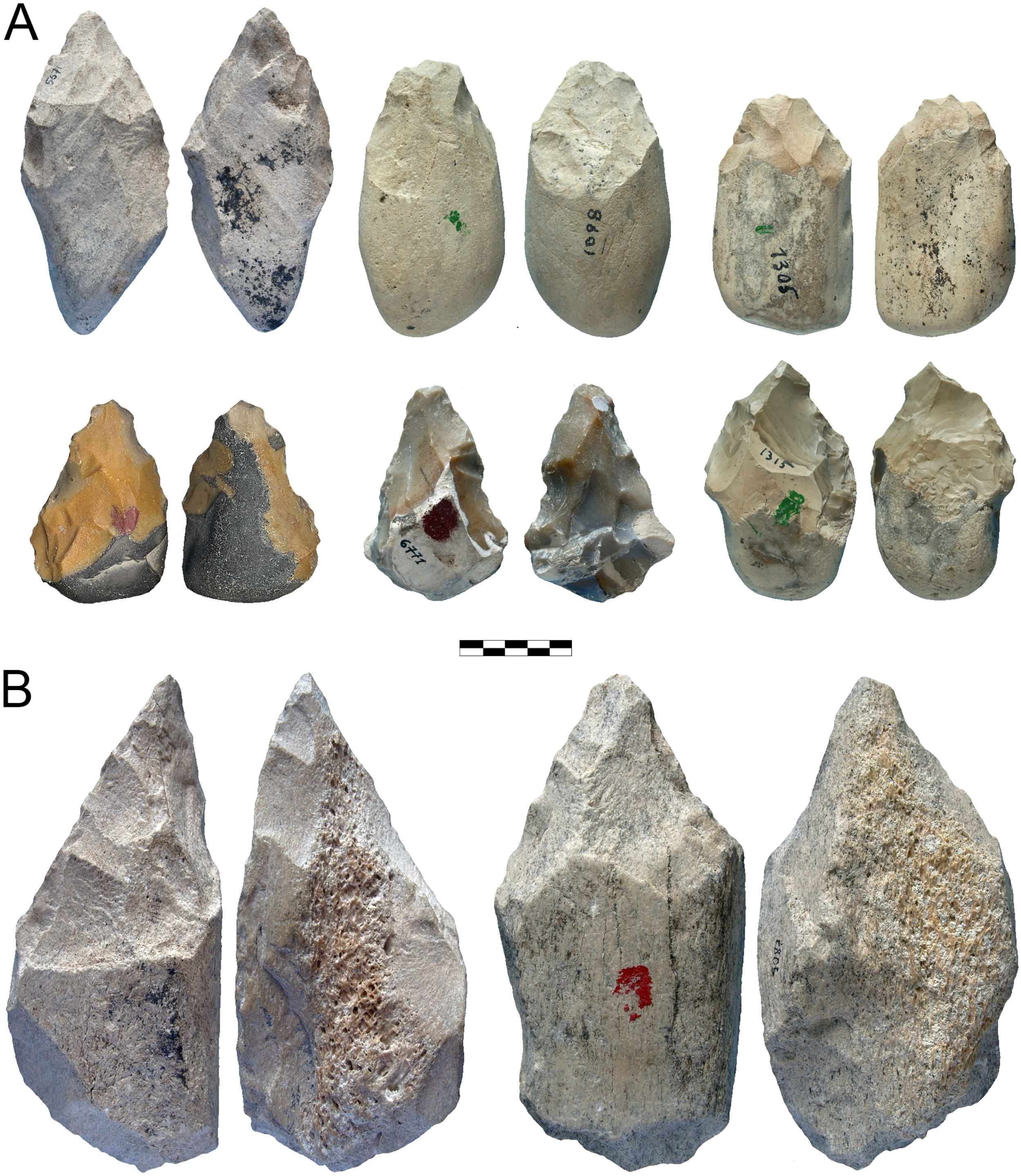
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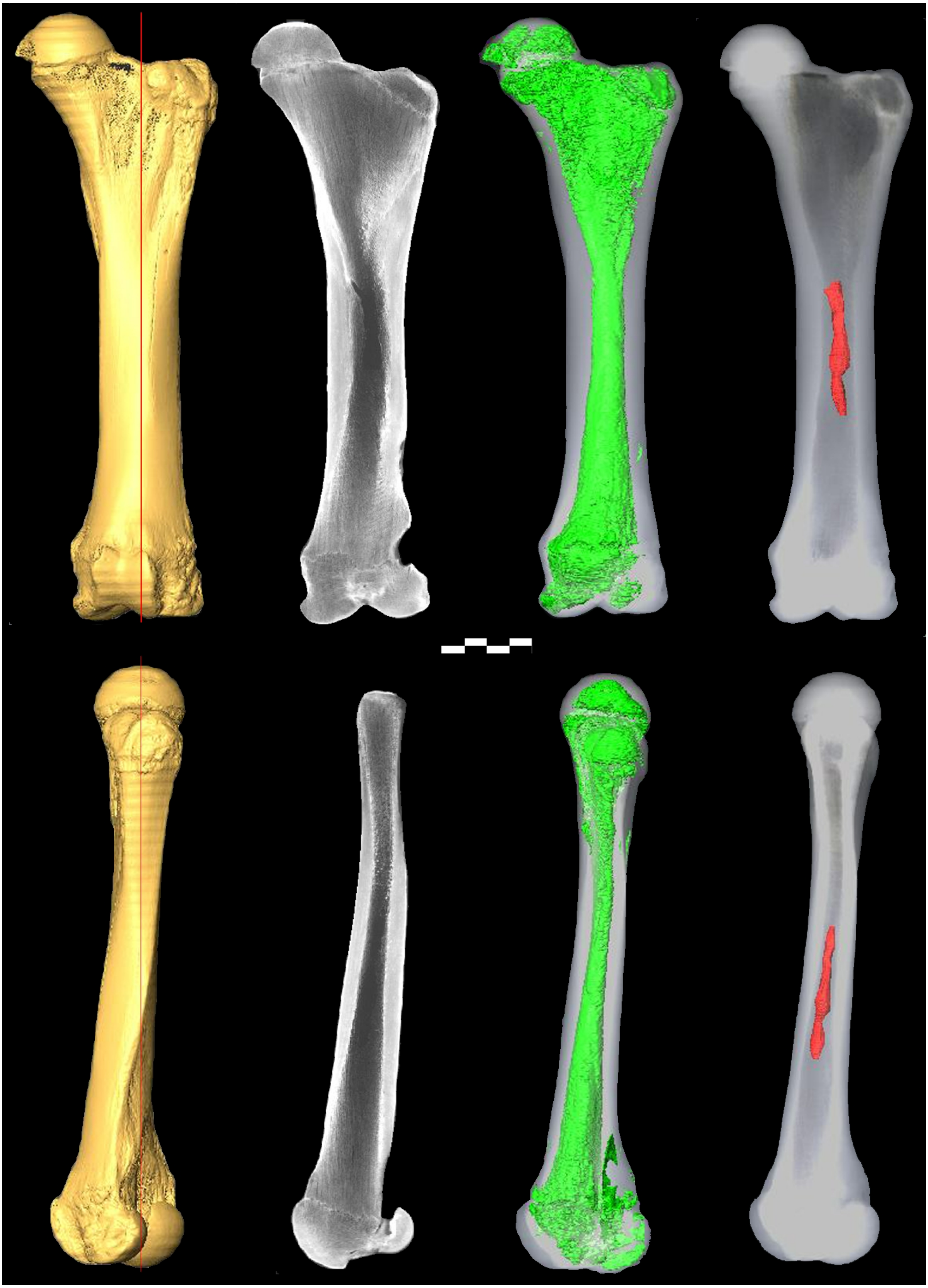

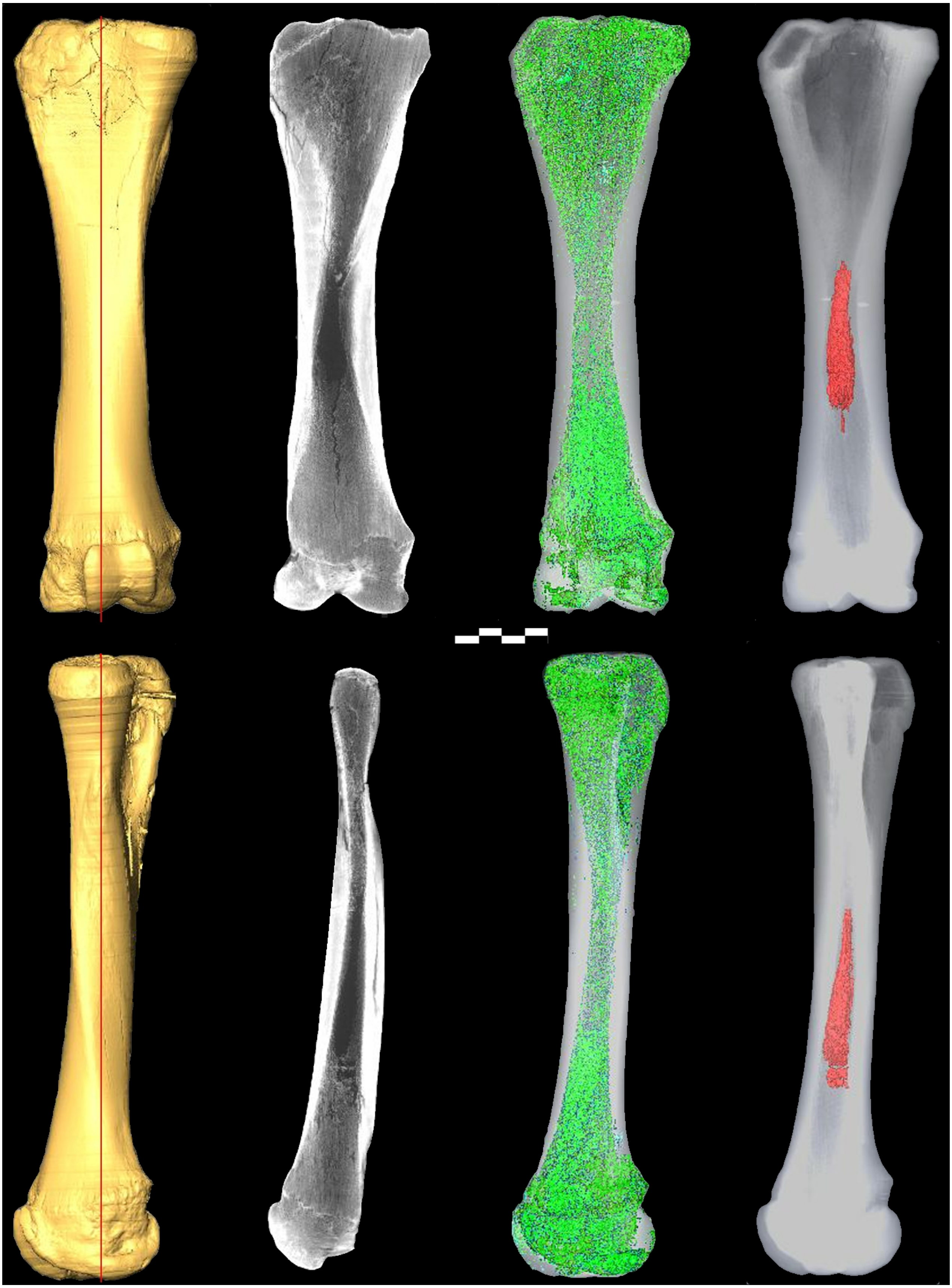

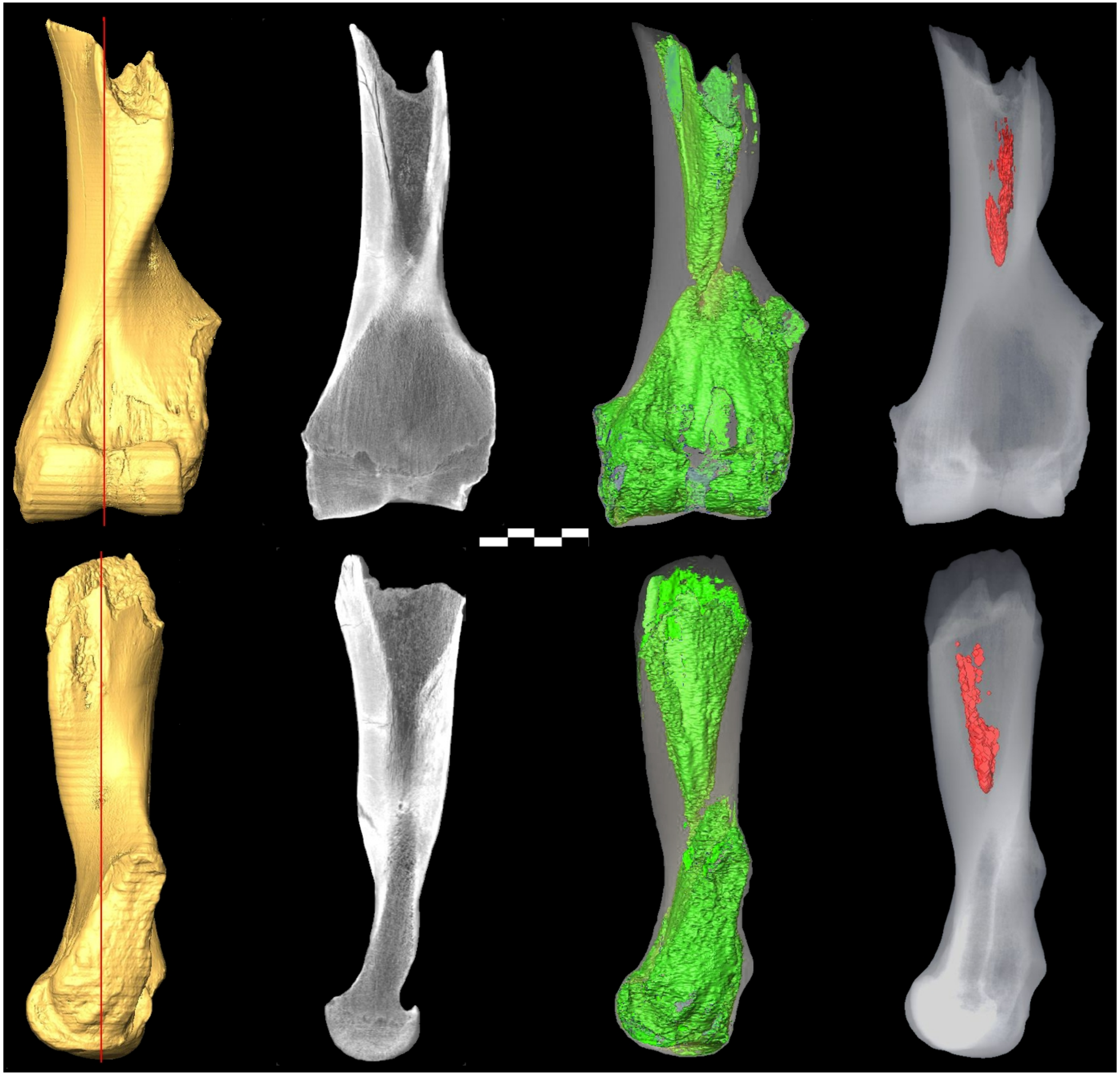

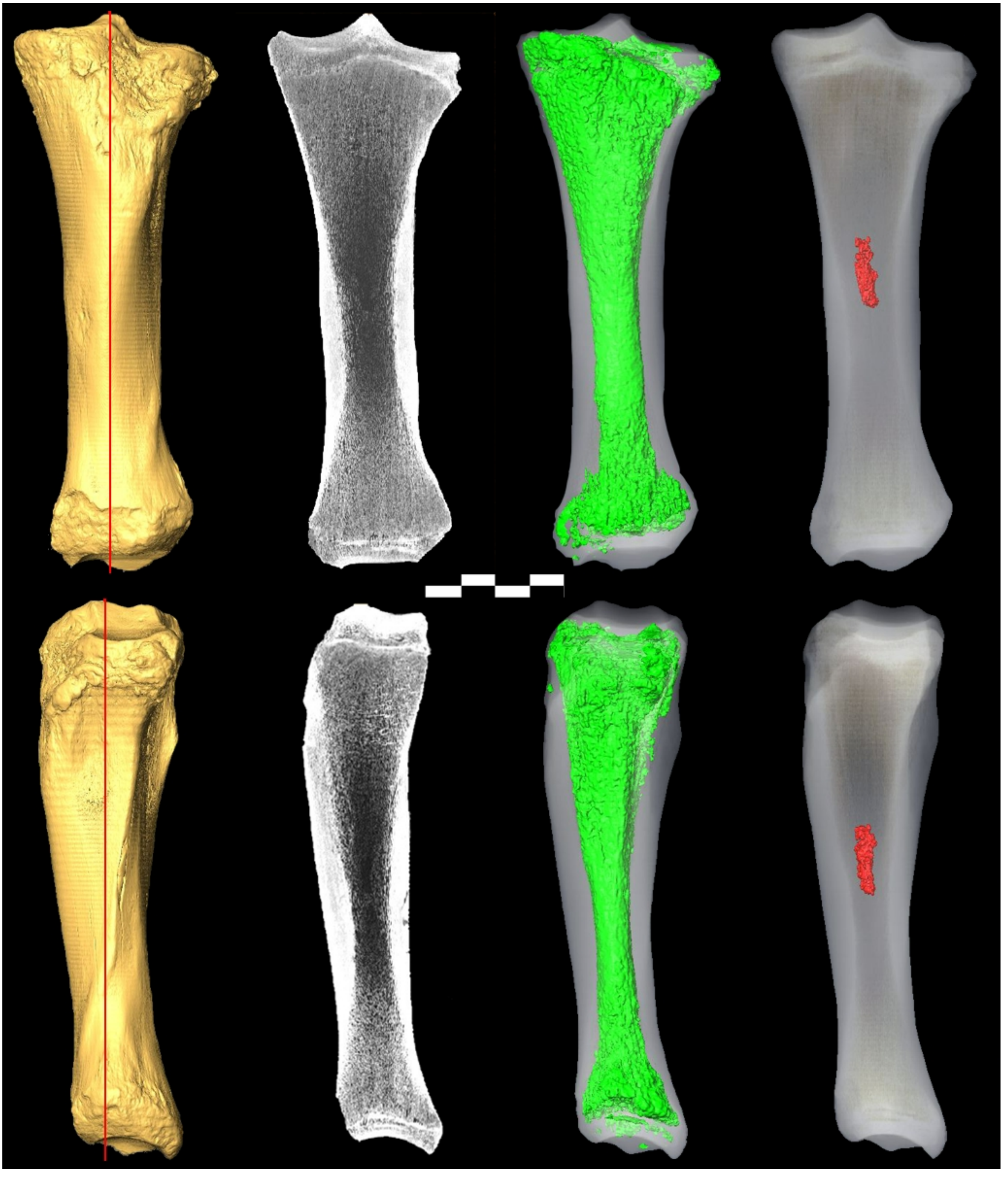

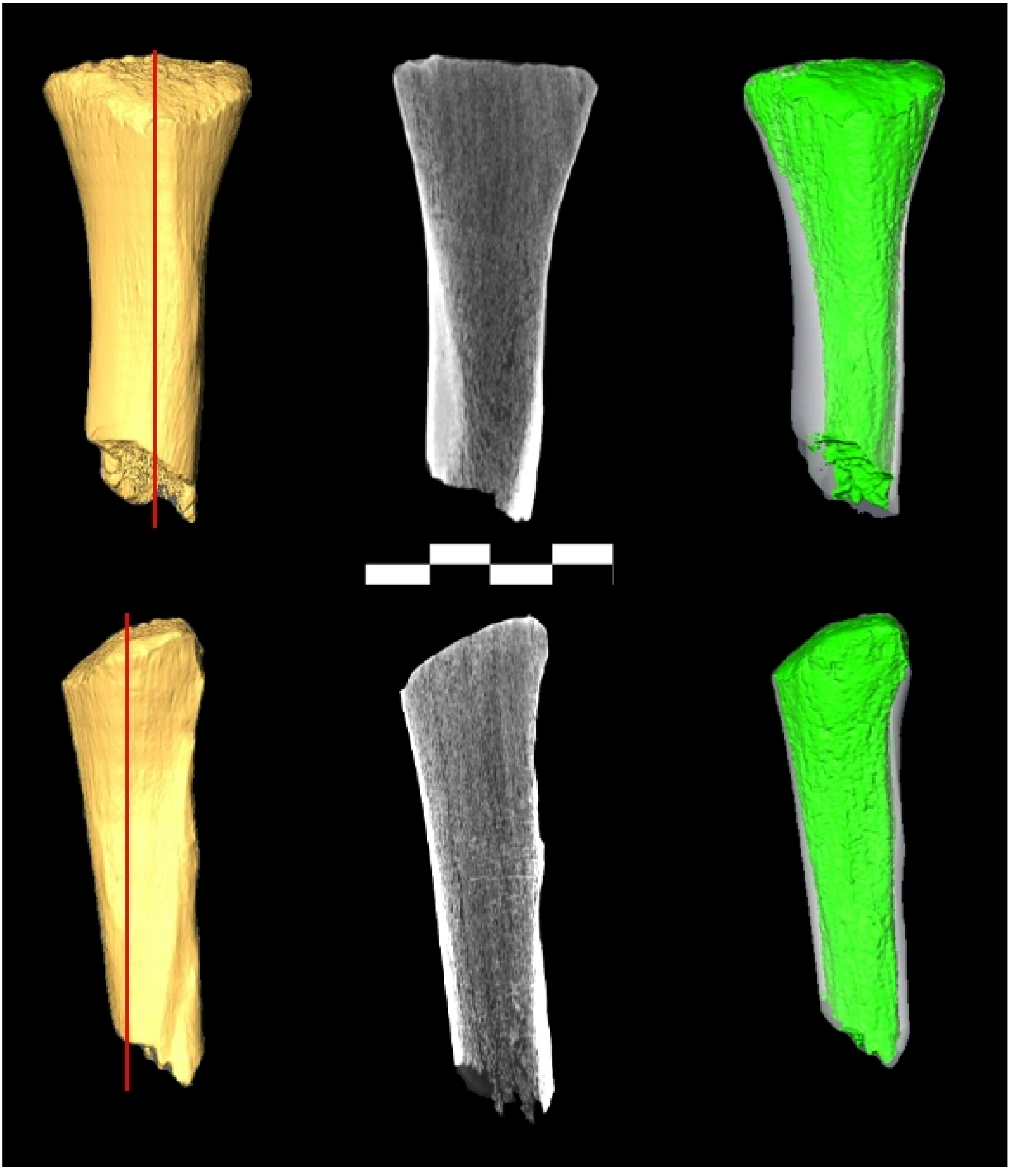

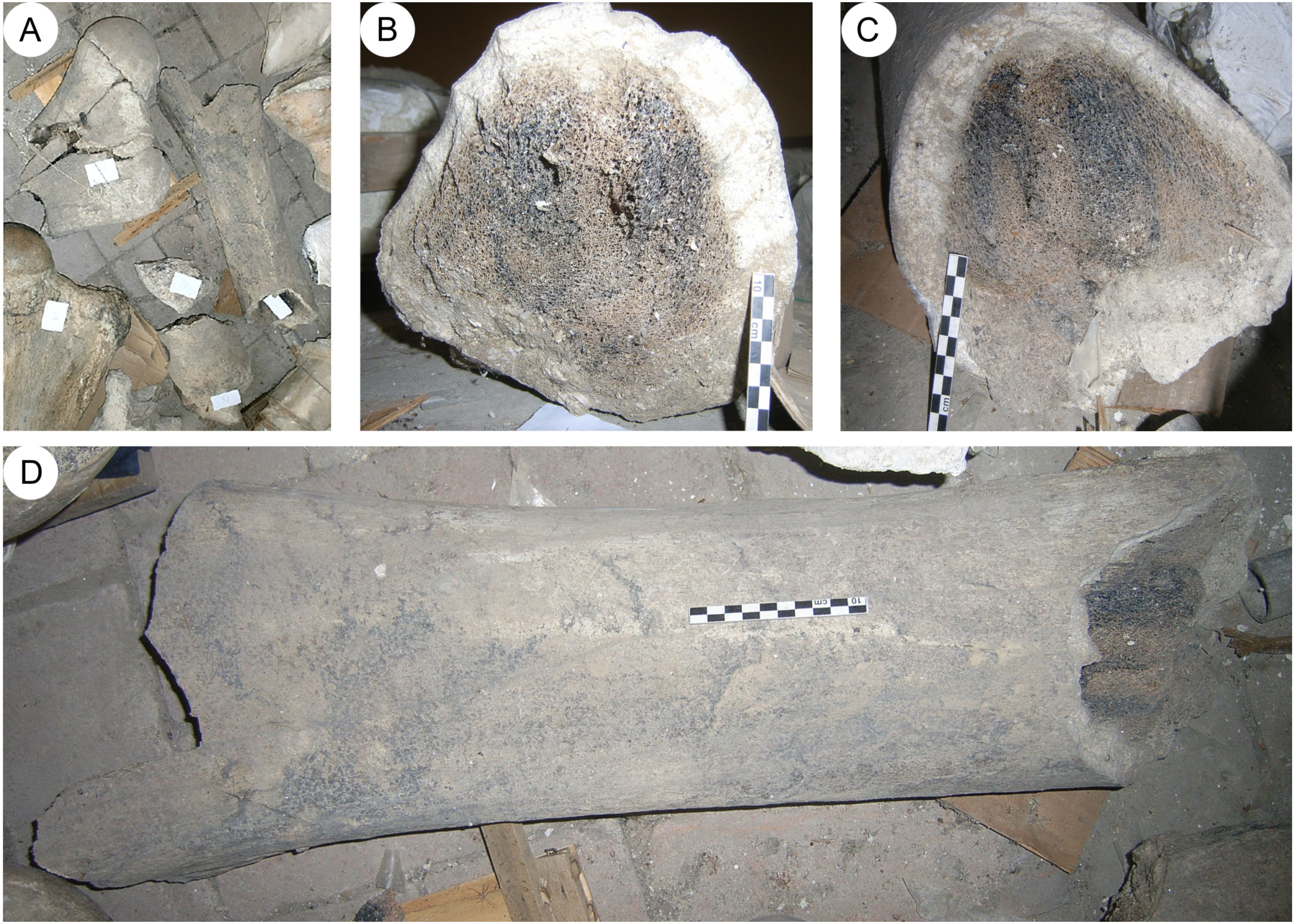
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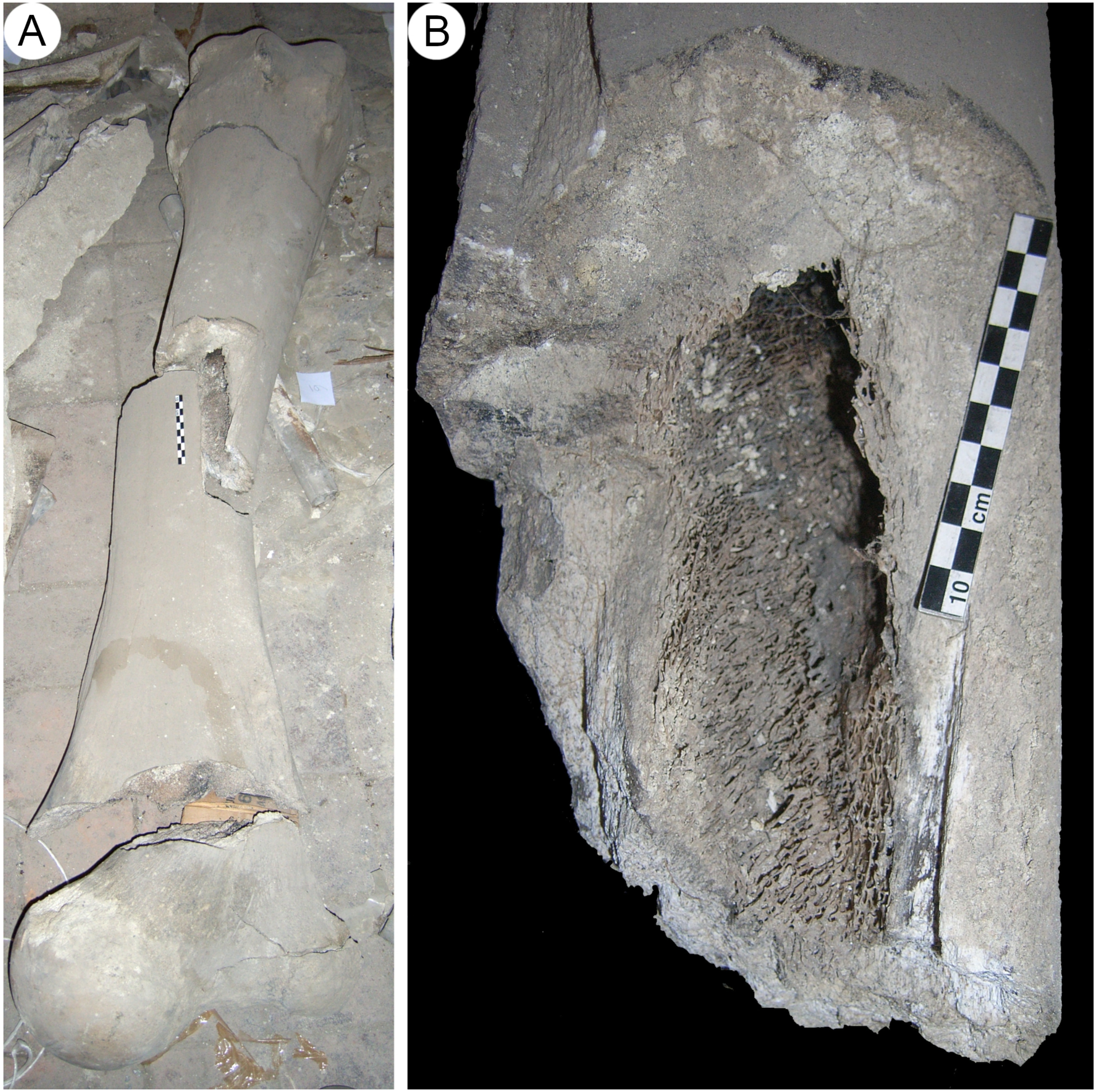
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NI	Anatomical ID	Portion preserved	Notes
CdG07	left humerus	proximal epiphysis	
CdG08	left humerus	distal epiphysis	
CdG36	left humerus	distal half	
CdG28	right humerus	distal epiphysis	
CdG19	right ulna	complete	broken (2 pieces)
CdG26	left tibia	almost complete	
CdG43	right tibia	proximal half	unfused (absent) epiphysis
CdG29	left femur	complete	
CdG30	right femur	almost complete	unfused (absent) *caput ossis femoris*
CdG32	left femur	complete	broken (4 pieces), fragmented proximal epiphysis
CdG06	right femur	complete	broken (4 pieces)
CdG33	femur	distal epiphysis	fragment

Table 1. Full set of unprocessed *Palaeoloxodon antiquus* limb bones from Castel di Guido.

NI	Anatomical ID	Age (years)		Measures (cm)				
				Bp	Bd	GL	GLC	SD
CdG43	right tibia	<18-24	juv					
CdG26	left tibia	>18-24		30.0	21.0	82.8		13.6
CdG36	left humerus	>18-19			37.5			16.0
CdG29	left femur	>30 (25-32)		44.0	31.5	128.5	133.0	18.8
CdG30	right femur	<30 (32)			28.0	131.0		20.0

Table 2. CT-scanned *Palaeoloxodon antiquus* bones. Age estimates following C. Craig, unpublished data cited in Haynes (1991: Table A15, Appendix p. 351), referred to extant African elephants. Measures following Von den Driesch (1976); Bp: (greatest breadth of the proximal end; Bd: (greatest) breadth of the distal end; GL: greatest length; GLC: greatest length from *caput femoris*; SD: smallest breadth of diaphysis.

	Medullary cavity size (cm)		Volumes (cm^3)			
Bone ID	Width	Length	Marrow cavity	Spongy tissue	Compact tissue	Whole bone
CdG43	-	-	-	2632	1003	3634
CdG26	1.5	6.0	114	8893	7018	16026
CdG36	3.5-4.5	13.5 (26.2)	78	12978	13603	26660
CdG29	2.5 - 3.7	17.9	306	12280	25309	37895
CdG30	1.8 - 5.5	34.5	358	19370	18412	38139

Table 3. Distinct bone tissue and medullary cavity size and volumes. Measures of CdG43 and CdG36 refer respectively to the proximal and distal half of bones broken mid-diaphysis; CdG43 belongs to a juvenile individual and lacks the proximal epiphysis. The proximal epiphysis is also incomplete in CdG30.

Bone ID	Marrow	Spongy	Compact	Age (years)
CdG43	-	72.4	27.6	juv (<18-24)
CdG26	0.7	55.5	43.8	>18-24
CdG36	0.3	48.7	51.0	>18-19
CdG29	0.8	32.4	66.8	>30 (25-32)
CdG30	0.9	50.8	48.3	<30 (32)

Table 4. Volume percentage of medullary cavities, cancellous and compact bone tissues versus total bone volume and estimated individual age.