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Histomorphometric age assessment of the Boxgrove 1 tibial diaphysis

Histomorphometric analysis of a medial midshaft chip from the Middle Pleistocene (ca. 500 ka BP) hominid tibia from Boxgrove, U.K. provides a modal age-at-death estimate at the end of the fourth decade of life. This makes Boxgrove 1 one of the older known and systematically aged Middle Pleistocene hominid specimens, and it reinforces the pattern of an underrepresentation of older adults observed in Middle and Late Pleistocene archaic *Homo* samples.

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Introduction

The analysis of human evolutionary patterns during the Pleistocene would ideally benefit from a paleodemographic perspective, given that differential survival is one of the baselines of evolutionary processes. It is unlikely that one will ever have sufficiently large, well documented and representative samples of the original populations from single site levels in the Pleistocene to carry out such paleodemographic analysis. However, it is possible to estimate the ages-at-death of Pleistocene hominid remains through various techniques, depending upon preservation and curatorial concerns. Current analyses of later Middle and early Late Pleistocene archaic *Homo* mortality patterns (Trinkaus, 1995; Bermúdez de Castro & Nicolás, 1997; Bocquet-Appel & Arsuaga, 1999) have been useful in identifying potential demographic biases in the available samples, which in themselves provide insights into the paleobiology of these Pleistocene human lineages. It is in the context of this framework that we undertook a histomorphometric analysis of the Boxgrove 1 Middle Pleistocene human tibia, to assess its probable age-at-death in the absence of macroscopic skeletal and dental indicators of age.

Previous histomorphometric analyses of Middle and Late Pleistocene human diaphyseal remains (e.g., Thompson & Trinkaus, 1981; Trinkaus & Thompson, 1987; Abbott *et al.*, 1996; Goldman *et al.*, 1996; Pfeiffer & Zehr, 1996; Ramsay, 1997; Streeter *et al.*, 2000) have documented histological patterns in femoral and tibial specimens similar to those of recent humans and a general consistency between the derived ages-at-death and macroscopic age indicators from associated remains. Of these specimens, only one, the Broken Hill EM-793 femur, is likely to approach the geological age of the Boxgrove specimen. The Boxgrove 1 analysis is intended in part as a contribution to

this growing body of histological data on these archaic and early modern humans.

The Boxgrove 1 tibia

In 1993 a largely complete hominid left tibial diaphysis was recovered from the site of Boxgrove, southern England (Gamble, 1994; Roberts *et al.*, 1994). The site at Boxgrove is located within a large sand and gravel quarry, situated ca. 10 km from the present English Channel coast, at the foot of the South Downs (Roberts *et al.*, 1997; Roberts & Parfitt, 1999). The fossil tibia was excavated from highly calcareous colluvial sediments that exhibit an erosive contact with underlying freshwater deposits (Roberts *et al.*, n.d.). A line of springs that emanated from a relict chalk sea cliff, some 50 m to the north of the site, provided the source of fresh water. The spring-water cut shallow channels and ponds in the conventional Boxgrove stratigraphic sequence (Stringer *et al.*, 1998; Roberts & Parfitt, 1999); these features were eventually infilled with reworked marine silt (the Slindon Silts), calcareous spring sediments and colluvial deposits. The tibia was found in association with flint débitage, resulting from the manufacture of Acheulian handaxes. Refitting of the lithics indicates that some of the material is derived from the underlying freshwater beds (Roberts *et al.*, n.d.). It is not possible as yet to ascertain whether the tibia was reworked from this source or if it was directly deposited within its parent sediment body. The freshwater beds and their temporal correlatives in the standard Boxgrove sequence are dated, using mammalian biostratigraphy, to the latter part of an early Middle Pleistocene interglacial. The colluvial sediment body containing the tibia was probably deposited at the beginning of the ensuing cold stage or glacial. The Boxgrove temperate sediments have been assigned to the last interglacial of the Cromerian Complex and the

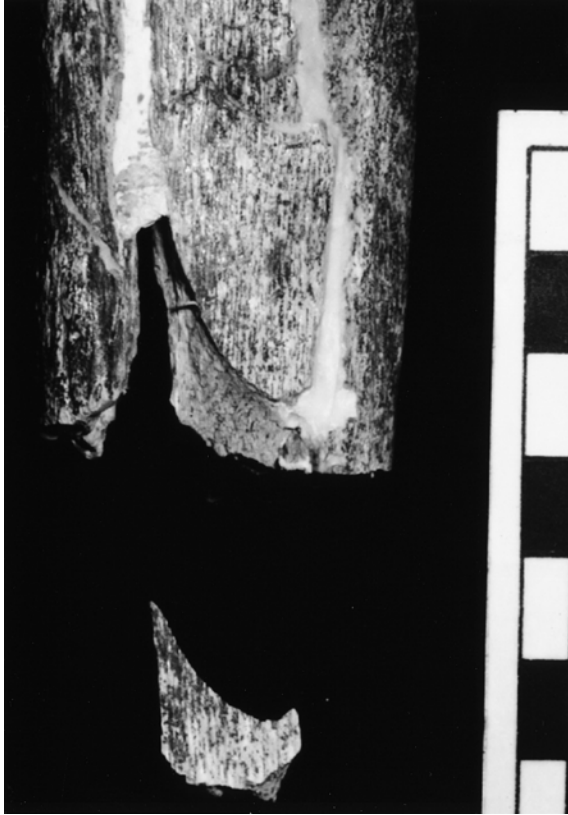


Figure 1. Photograph of the Boxgrove 1 tibial medial midshaft, showing the shaft chip employed for the histological assessment and its position on the shaft. The distal end of the proximal half of the diaphysis is shown in medial view above, and the transverse fossilization break at its distal end is close to midshaft. The detached chip of bone analyzed histologically is located below it. Scale in centimeters.

overlying periglacial sediments to the Anglian Cold Stage (Preece & Parfitt, 2000). The Boxgrove 1 tibia is therefore approximately the same age as the Mauer 1 mandible, and it probably represents one of the earliest human populations to enter trans-Alpine Europe (Roebroeks & van Kolfschoten, 1994; Dennell & Roebroeks, 1996; Gamble, 1999). Morphological (Stringer *et al.*, 1998) and biomechanical (Trinkaus *et al.*, 1999) analysis of Boxgrove 1 tibia indicate that it is similar to other Pleistocene archaic *Homo* tibiae in its external morphology and overall robusticity, and that it probably derived from an indi-

vidual with relatively stocky, cool-adapted ecogeographic body proportions.

The distal half of the Boxgrove tibial diaphysis was largely intact, but the bone was broken transversely at midshaft post mortem, and the proximal half was reassembled along vertical breaks from several portions (Stringer *et al.*, 1998). One of the detached pieces is a small flake of medial cortical bone, extending proximally from the transverse break, which remained separate from the reassembled diaphysis (Figure 1). This flake of tibial cortical bone, approximately triangular in shape, measured 26.7 mm in length and 16.5 mm at the

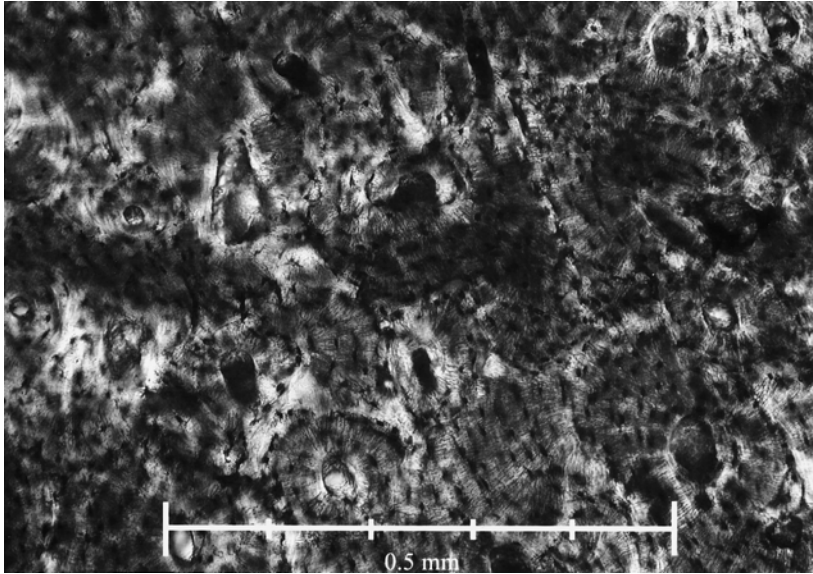


Figure 2. A typical microscopic field of cortical diaphyseal bone from the Boxgrove 1 tibia. The field shown is representative of the state of preservation of the cortical bone microstructures contained in the medial fragment, showing the preservation of the osteons, the Haversian canals, and the associated structures. The scale measures 0.5 mm in total length.

widest part. The maximum cortical thickness of the fragment is 4 mm, measured from the microscopically observable endosteal circumferential lamellae to the outer surface of the cortex. The fragment was sectioned and examined histomorphometrically (Figure 2). Even though its microstructure shows some diagenetic effects, the changes had little effect on the visibility of the primary histological (osteonal) structures, and therefore histomorphological analysis was possible. It is this small flake of bone that has been employed for microstructural examination.

Methods

The bone fragment from Boxgrove 1 presents an unusual situation for age assessment, because the tibia is the only skeletal element recovered for this individual. As a result, the individual's age-at-death cannot be assessed by macroscopic methods, and it must be evaluated through histological

means. The only other human remains from the site, the Boxgrove 2 mandibular incisors, derive from a lower stratigraphic level and almost certainly from a second individual.

The Boxgrove 1 tibial fragment was embedded in a resin medium, Castolite[®] (Buehler Ltd, Evanston, IL, U.S.A.) to secure the integrity of the bone during sectioning and grinding. Transverse sections approximately 100 μm thick were cut using a low-speed Isomet metallurgical saw with a diamond embedded blade (Buehler Instruments, Evanston, IL, U.S.A.). The resulting seven sections were then hand ground, using 400 grit silicon carbide sandpaper, to a thickness of approximately 80 μm . The sections were mounted on standard microscopic slides and cover-slipped. A research microscope with a 10 \times objective and matched 10 \times oculars fitted with a Merz counting reticule (Merz & Schenk, 1970) was used to perform area measurements and osteon counts as described in Anderson (1982). Because of the very small

Table 1 Regression formulae employed to estimate the age-at-death of Boxgrove 1

Bone	Formula	Reference
Tibia	Age = 1.285 (<i>n.On</i>) + 23.22 (± 8.5 yr)*	Thompson & Galvin (1983)
Tibia	Age = 75.93 (<i>On.Ar</i>) (<i>n.On</i>) + 25.966†	Thompson (1979)

**n.On*: The number of whole osteons per mm².

†*On.Ar*: The mean area of whole osteons in mm².

area available for analysis, osteon and area measurements were derived by sampling across the entire surfaces of all seven sections from the Boxgrove tibial fragment.

The histological methods developed for estimating age-at-death are bone specific. Several age estimation methods for use on the tibia have been proposed (Kerley & Ubelaker, 1978; Thompson, 1979; Thompson & Galvin, 1983; Uytterschaut, 1985) with Kerley & Ubelaker's method (1978) being most widely used by biological anthropologists. However, Kerley & Ubelaker's method (1978), as with most other methods, requires a complete cross-section of bone or a specific area of the tibia that is not available from the Boxgrove tibia. The small size of the fragment and the medial location of its origin preclude the use of any of these methods and allows only the application of the sampling method developed by Thompson (1979).

Concerned about the impracticability and unacceptability of taking complete cross-sections of bone from valuable archaeological material, Thompson (1979) developed a method that is less destructive, requiring removal of only a small core 4 mm in diameter. Measurements were averaged over three adjacent fields at 100 × . Because subsequent application of the original tibial regression formula (Thompson, 1979) found it to overestimate age, a new formula was proposed by Thompson & Galvin (1983). The new formula utilized only the number of whole secondary osteons per mm² (*n.On*), which proved to be the best predictor of age in individuals less than

55 years. The location specified for histomorphometric examination of the tibia in Thompson & Galvin's method (1983) is medial midshaft, which, fortunately, is the same location as the Boxgrove tibial fragment. The total area of bone that is required for the Thompson & Galvin method (3 mm²) is included within the cross-sectional area of cortical bone (10.7 mm²) available from the Boxgrove 1 fragment (Table 1).

Results

Microscopic examination of the fragment of bone from the tibia of Boxgrove reveals substantial histomorphological preservation and virtually all fields are readable. Distinct histomorphological features, such as osteons and osteon fragments, are sufficiently identifiable and quantifiable to permit an histomorphometric age assessment of these remains (Figure 2). Application of the Thompson & Galvin (1983) predicting formula yields an estimate of the age-at-death of 39.5 years with a range of 31.0–48.0 years for the Boxgrove tibia. The earlier Thompson (1979) formula provides a much higher age (62.6 years ± 8.9 years) (Table 2).

Discussion and conclusions

For comparison, histological ages from the Shanidar 2 early Late Pleistocene Neandertal tibia are also provided (Table 2). Macroscopic age indicators for Shanidar 2, in particular the degree of attrition of its

Table 2 Comparison of histomorphometric parameters obtained for the Boxgrove 1 and the Shanidar 2 tibiae

	Boxgrove 1	Shanidar 2
Parameters		
Mean osteon area (± 1 S.E. _{mean})	0.038 mm ² \pm 0.004	0.038 mm ² \pm 0.002
Osteon population density (± 1 S.E. _{mean})	17.9/mm ² \pm 0.57	11.5/mm ² \pm 0.53
Number of osteons (± 1 S.E. _{mean})*	12.7/mm ² \pm 0.40	10.1/mm ² †
Histological age (± 1 S.E. _{est})		
Thompson (1979)	62.6 \pm 8.9 yrs	55.1 \pm 8.9 yrs
Thompson & Galvin (1983)	39.5 \pm 8.5 yrs	36.2 \pm 8.5 yrs

*The number of whole (intact) osteons per mm².

†The number of whole osteons was extrapolated from the percent osteonal bone given in Table 3 of *Abbott et al. (1996)*.

complete dentition compared to those of otherwise aged late archaic human specimens from Shanidar and other sites, indicate a young adult age, most likely during the third decade of life (*Trinkaus, 1983*). Our histomorphometric age estimate using the *Thompson & Galvin (1983)* formula yields a slightly older age but the probable range encompasses the macroscopic age estimate for this individual. This correspondence provides confidence that the age estimate for Boxgrove 1 in the fourth or early fifth decade of life is appropriate. If anything, the older histomorphometric age, as opposed to dental attrition age-at-death, for Shanidar 2, may suggest that the histomorphometric age for Boxgrove 1 is slightly overestimating its actual age-at-death.

Morphological and biomechanical analysis suggest higher levels of habitual mechanical loads on the lower limbs in Pleistocene hominids, such as Boxgrove, relative to modern humans (*Stringer et al., 1998; Trinkaus et al., 1999*). It is possible that the resultant higher habitual strain levels resulted in higher rates of osteon creations (Ac.F). This is supported by the work of *Robling (1998)* in which osteon counts (OPD) in the femur were observed to increase relative to the rib with increased mechanical loading. If applicable to this situation, it would explain the slightly higher

mean histological age estimate for Shanidar 2 and suggest that this technique may be modestly overestimating the age-at-death of Boxgrove 1.

Further support for the consistency of the *Thompson & Galvin (1983)* tibial equations comes from comparison of mean osteon area between the Shanidar 2 and the Boxgrove 1 tibiae. Osteon area appears to correlate with age (*Currey, 1964*). Since osteon size for both tibiae has been measured to be 0.038 mm², the two Pleistocene hominid tibiae may have belonged to individuals of a similar age.

The resultant age-at-death estimates for Boxgrove 1 towards the end of the fourth decade of life make this individual one of the older known Middle Pleistocene hominids, judging from the paucity of individuals from other Middle or initial Late Pleistocene sites who passed even the third decade of life. This is especially apparent in the three largest samples, Atapuerca-SH, Krapina and Zhou-Kou-Dian (*Weidenreich, 1937; Wolpoff, 1979; Bermúdez de Castro & Nicolás, 1997; Bocquet-Appel & Arsuaga, 1999*). Based on dental attrition, there are only a few other individuals known from this time period that are likely to have achieved similar ages, including those represented by the Arago 2 mandible, the Broken Hill 1 cranium, the Salé 1 cranium, and the

Thomas 1 mandible. In contrast, by the Late Pleistocene there are a number of archaic humans known who appear to have lived well into the fifth or even the sixth decade (Trinkaus, 1995). Moreover, it is likely, given demographic considerations, that older individuals are underrepresented in those later samples (Trinkaus, 1995). However, this same underrepresentation would apply to currently known Middle Pleistocene hominid samples.

This analysis, as well as previous mortality assessments of later Pleistocene humans (e.g., Wolpoff, 1979; Trinkaus & Thompson, 1987; Trinkaus, 1995), assumes that the life-history segment lengths of the population represented by Boxgrove 1 were similar to those of recent humans, upon whom the regression formulae employed are based. Later Middle and Late Pleistocene hominid intertooth relative dental calcification patterns (Tompkins, 1991, 1996) and degrees of encephalization (Ruff *et al.*, 1997) differed only slightly from those of recent humans. Given the reasonable close fit between dental formation and developmental patterns (Smith, 1991) on the one hand and the positive correlations between brain size and the lengths of life history segments (Harvey *et al.*, 1986) on the other, this assumption of similar life history parameters appears to be reasonable for Late Pleistocene hominids.

Adequate samples of earlier Middle Pleistocene immature hominid mandibles have yet to be analyzed from a dental calcification perspective, but the significant increase in brain size during the Middle Pleistocene (Ruff *et al.*, 1997), combined with the above mentioned correlation between brain size and life history segment lengths, suggests that the life history segments of earlier Middle Pleistocene specimens such as Boxgrove 1 may have been shorter on average than those of recent humans. This hypothesis remains untested, and how any difference (if present) might

affect age estimation from histomorphometric (or macroscopic) age indicators remains uncertain.

Regardless of the resolution of these issues regarding the calibration of age indicators among pre-Late Pleistocene archaic *Homo* populations, it is apparent that the known Middle Pleistocene hominid fossil record has an underrepresentation of older individuals, with the current record dominated by young adult and immature remains. Although a variety of taphonomic, behavioral and paleontological processes may contribute to this age bias in the sample, a combination of demographic stress and local population demographic instability may have been a major contributor to the observed pattern (see discussion in Trinkaus, 1995).

At the same time, the present study has shown that histomorphometric methods provide a means to estimate the age-at-death of fragmentary paleontological material such as the Boxgrove 1 tibia. The application of these methods to large samples of Middle Pleistocene archaic *Homo* where other aging methods can be employed (e.g., the Atapuerca-SH sample) is therefore highly desirable and would help both to refine the level of consistency of these histomorphometric methods with other approaches and expand our paleobiological assessments of these archaic hominids.

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