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*paranthropus robustus*



## Microbial osteolysis in an Early Pleistocene hominin (*Paranthropus robustus*) from Swartkrans, South Africa

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### ABSTRACT

Microbiological degradation is one of the most important factors responsible for the destruction of bone in archaeological contexts. Microscopic focal destruction (MFD) is the most prevalent form of microbial tunneling and is encountered very commonly in human bones from archaeological sites, whereas animal bones from these same sites show significantly better preservation if they were deposited in a fragmentary (e.g., butchered) state. Similarly, most fossils show either no evidence or only minor traces of bacterial osteolysis. These observations and experimental evidence point to an endogenous origin for osteolytic bacteria, suggesting that bone bioerosion could potentially aid in reconstructing early taphonomic events. We here report extensive MFD in the mandibular corpus of a small (presumptive female) individual of the hominin *Paranthropus robustus* from the Early Pleistocene site of Swartkrans, South Africa. The specimen (SKX 5013) derives *in situ* from the Member 2 deposit, which is dated to ca. 1.5–1.0 Ma. Examination of sections from the corpus by backscattered electron microscopy reveals numerous small linear longitudinal and budded tunneling cavities, which tend to be concentrated around Haversian canals and are more abundant closer to the endosteal aspect of the section. The taphonomy of Swartkrans has been the subject of intense investigation, and given the possibility that different agents of accumulation may have been responsible for the faunal and hominin fossils in the different members at the site, the observation that a specimen of *P. robustus* from Member 2 displays significant microbial osteolysis is of potential interest. A study of the prevalence of this process in adequately large samples of the animal bones from these units may yield novel insights and provide refinement of our understanding of their taphonomic histories. Such observations might well reveal differences among the various members that could provide another valuable source of osteo-archaeological information for the site.

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### 1. Introduction

The survival of bone in terrestrial palaeontological and archaeological contexts is dependent upon a variety of factors, including climate (temperature and rainfall), length of surface exposure

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before burial, soil characteristics (including pH, moisture regime, texture, and organic component), and biodegradation (White and Hannus, 1983; Pate and Hutton, 1988; Tappen, 1994; Hedges and Milliard, 1995; Nicholson, 1996; Andrews and Armour-Chelu, 1998; Nielsen-Marsh and Hedges, 2000; Pike et al., 2001; Jans et al., 2002; Trueman et al., 2004; Nielsen-Marsh et al., 2007; Smith et al., 2005, 2007; Fernández-Jalvo et al., 2010). In many environments, biodegradation is more rapid and pervasive than chemical deterioration, and its effects may be more pronounced (Hedges, 2002; Trueman and Martill, 2002; Turner-Walker, 2012). Indeed,

among the factors responsible for the destruction of bone in archaeological contexts, microbiological degradation appears to be the most important. Common agents of bioerosion include fungi, cyanobacteria, and bacteria.

The study of the damage inflicted by bioerosive agents has a long history, dating to Wedl's (1864) description of the elaborate branching tunnels produced by fungi and cyanobacteria (Marchiafava et al., 1974). Hackett (1981) described types of what he termed "microscopical focal destruction" (MFD)—linear longitudinal, budded, and lamellate chambers—that appear to be the products of bacterial erosion (Child, 1995; Jans, 2008). Davis (1997) and Trueman and Martill (2002) expanded upon Hackett's (1981) descriptive classification of various tunneling types, and most recently Pirrone et al. (2014) have compiled an elaborate ichnotaxonomy of these "trace fossils" based on the morphology of the bioerosive cavity.

Wedl-type branching tunnels occur extensively if not exclusively along the periosteal margins of bones, whereas non-Wedl MFD commonly occurs around vascular (e.g., Haversian) canals (Turner-Walker et al., 2002).

Non-Wedl MFD is the most prevalent form of microbial tunneling and is encountered very commonly in human bones from archaeological contexts (Turner-Walker et al., 2002; Jans et al., 2004; White and Booth, 2014). By comparison, animal bones from these same sites show significantly better preservation if they were deposited in a fragmentary (e.g., butchered) state (Jans et al., 2004; Nielsen-Marsh et al., 2007). This observation has been employed to implicate endogenous bacteria as principal osteolytic agents. Bacterial attack of bone has been reported for hominins from the ca. 400,000 year-old site of Sima de los Huesos, Sierra de Atapuerca, as well as Late Pleistocene mammoths and Cretaceous dinosaurs (Bromage and Perez Ochoa, 2009; Lam et al., 2009; Kremer et al., 2012; Rogoz et al., 2012). It has also been observed in the orthodontine of some fossil mammal teeth (Fostowicz-Frelik and Frelik, 2010; Kalhoff et al., 2011). However, most fossils show either no evidence or only minor traces of such osteolysis (Trueman and Martill, 2002; Chinsamy-Turan, 2005; Farlow and Argast, 2006).

Bacteria have been implicated as the agents responsible for MFD (Baud and Lacotte, 1984; Yoshino et al., 1991; Child et al., 1993). As noted by White and Booth (2014), there has been some debate as to whether the bacteria that are primarily responsible for non-Wedl MFD of bone are intrinsic to an organism (endogenous) or originate from the burial soils (exogenous). Certainly, bacteria are numerous in soils (Gans et al., 2005; Fierer and Jackson, 2006), and many of these are capable of producing enzymes such as collagenase. Collagenase catabolizes collagen by unwinding it and cleaving its polypeptide bonds (Sellers and Murphy, 1981; Chung et al., 2004), and the breakdown of collagen is an important step in the dissolution of bone (Child et al., 1993; Hedges, 2002; Trueman and Martill, 2002). Some research has supported the exogenous model, observing that bones retain structural integrity until skeletonization, at which point they begin to undergo bioerosion from bacteria in the sedimentary environment (Grupe and Dreses-Werringloer, 1993; Balzer et al., 1997; Fernández-Jalvo et al., 2010). In support of this, Dixon et al. (2008) inoculated 700 year-old human femoral fragments with *Prevotella intermedia*, a bacterium that is prevalent in soils and also a pathogen in the human oral microbiota. They maintained their samples at 4 °C so as to resemble soil temperature, and although this is well below the optimum of 37 °C for growth and development of this bacterium, they found significant MFD after only 33 weeks of exposure. Unfortunately, the small fragments of bone comprising that study's sample do not mimic the complete bones of human burials.

On the basis of the morphology of the sub-micron spongiform pores of MFD chambers, Jackes et al. (2001) suggested *Clostridium*

*histolyticum* as perhaps the best bacterial candidate for the dissolution of bone. This species occurs in the intestines of humans and other mammals, and produces collagenase. Because bones that derive from complete burials are more likely than fragmented elements to be affected by bacterial attack, it has been argued that this implicates the activity of endogenous bacteria that travel from the intestinal tract through the vascular system during putrefaction (Bell et al., 1996; Jans et al., 2004; Nielsen-Marsh et al., 2007; Hollund et al., 2012).

An endogenous origin for osteolytic bacteria would then suggest that bone bioerosion may reflect the extent to which a given skeletal element was exposed to putrefaction in the early post mortem period (White and Booth, 2014). As such, measures of bone bioerosion could potentially aid in reconstructing early taphonomic events (Bell et al., 1996; Turner-Walker and Jans, 2008; Hollund et al., 2012). The experimental work by White and Booth (2014) has provided substantial support for the primary involvement of endogenous bacteria.

Microbial attack can potentially affect a variety of analyses ranging from those on stable light isotopes (Balzer et al., 1997; Scharlotta et al., 2013) to ancient DNA (Willerslev and Cooper, 2005; Marciniak et al., 2015). Bioerosion may also profoundly affect histomorphometric analyses of bone remodeling (Dempster, 2008), such as those related to species identification (Dominguez and Crowder, 2012), ontogenetic age determination (Robling and Stout, 2008), and activity patterns (Carter, 1984; Burr et al., 1985; Pearson and Lieberman, 2004; Pfeiffer et al., 2006).

Indeed, an attempt to investigate cortical bone remodeling in the mandibular corpus of the Early Pleistocene hominin *Paranthropus robustus* from the site of Swartkrans, South Africa led to the present documentation of microbial attack in this fossil. To our knowledge, this is the first fossil hominin specimen of this antiquity in which MFD has been identified. We present this case report in light of the comparative rarity of bioerosion in the palaeontological record, and in view of the possible implications that it might have for taphonomic interpretations at this site. In order to place these potential taphonomic implications in context, we provide a brief review of the temporal and archaeological differences among the various fossiliferous deposits at the site of Swartkrans.

## 2. Swartkrans

Swartkrans (25°58'08"S; 27°45'21"E) is a palaeokarst cave that developed in Precambrian dolomitic limestone. The cave infilling comprises calcified and unconsolidated sediments that derived from the surface. These deposits contain a large number of faunal elements as well as both lithic and bone artifacts. The site has yielded a small number of early *Homo* remains but is best known for its abundant *P. robustus* fossils.

Butzer (1976) designated the fossiliferous breccias as the Swartkrans Formation and recognized two stratigraphic units. Subsequent work by Brain (1993b) documented the existence of five members in a complex arrangement developed through a number of depositional and erosional cycles. Members 1 through 3 have been the subject of intense investigation owing to their richness in hominin fossils and archaeological debris. Member 4 is a colluvial deposit that contains Middle Stone Age artifacts but is devoid of bone. Sutton et al. (2009) have suggested that the absence of bone in this unit may indicate the lack of a cave roof over the area in which it was deposited.

The oldest fossil-bearing sediments have been designated as Member 1. This is the most extensive deposit and is divisible into "Hanging Remnant" (HR) and "Lower Bank" (LB) components. The former consists of calcified cave 'breccias' (the so-called Pink Breccia), whereas most of the latter is represented by decalcified

(or uncalcified) sediments. Member 2 sediments are both calcified (the so-called Brown Breccia) and either decalcified or uncalcified. Member 3 is largely uncalcified. Abundant fossils of *P. robustus* have been recovered from Member 1, and this species is also reasonably well-represented in Members 2 and 3 (Grine, 1989). Craniodental remains attributable to the genus *Homo* have been recovered from Members 1 and 2. A few postcranial bones are the only specimens that have been attributed to *Homo* from Member 3 (Grine, 2005).

A variety of methods have been applied in attempts to determine the geochronology of the site. Electron spin resonance (ESR) studies on tooth enamel (Blackwell, 1994; Curnoe et al., 2001) have produced a preposterously broad range of dates—4.38–0.36 Ma—for the three fossiliferous members. Substantially more reasonable age ranges of about 2.0–1.6 Ma for Member 1, 1.5–1.0 Ma for Member 2, and approximately 1.0–0.8 Ma for Member 3 are indicated by palaeontological correlation (Brain, 1993b; McKee et al., 1995; Vrba, 1995), U–Pb studies of bovid tooth enamel (Balter et al., 2008) and speleothems (R. Pickering et al., 2011), and analysis of buried cosmogenic nuclides (Gibbon et al., 2014).

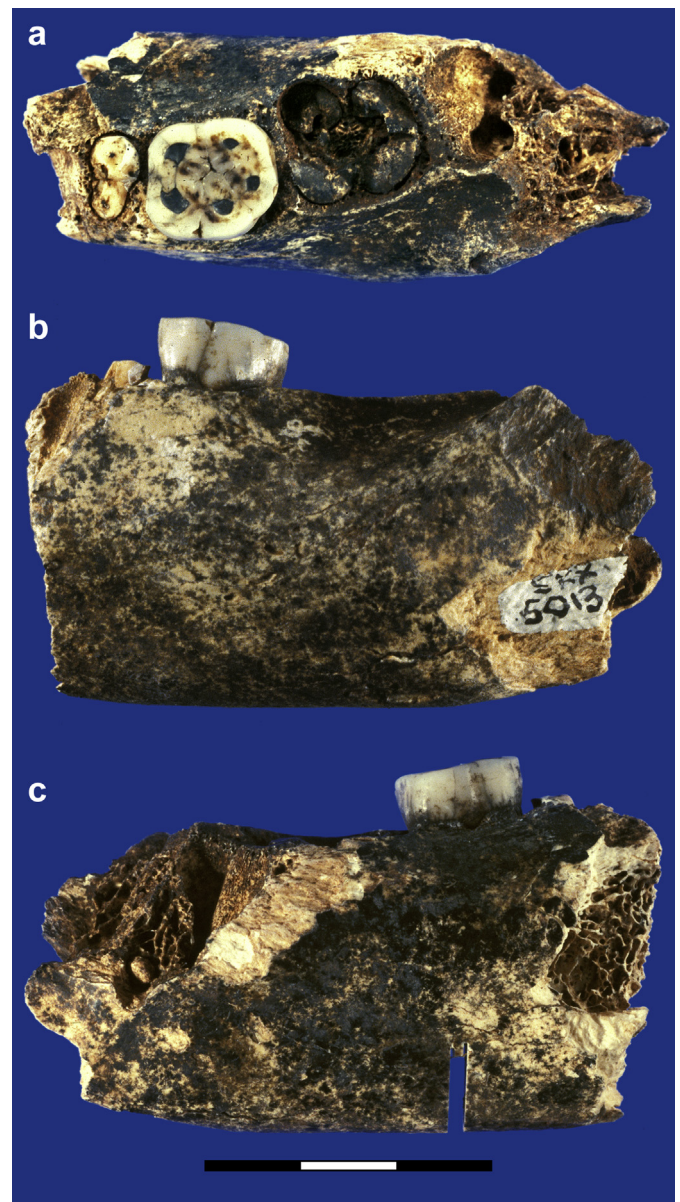
With reference to the archaeological record, Members 1, 2, and 3 have yielded numerous stone tools (Clark, 1993) and close to 84 bovid limb bones and horn cores that were utilized in digging activities (Brain, 1989; Brain and Shipman, 1993; Backwell and d'Errico, 2001; d'Errico and Backwell, 2003). Clark (1993) has posited that while the stone tools from these three units can be assigned to the “core/chopper/flake” tradition, the assemblage from Member 1 differs from those in Members 2 and 3. The latter contain larger flakes, examples (albeit rare) of cores that had been bifacially worked, and evidence of change in raw material emphasis from chert to quartz. Clark (1993) suggested that the Member 1 lithic artifacts are attributable to the Oldowan or Developed Oldowan, while those from Members 2 and 3 represent the early Acheulean. Similarly, the animal bones seem to reveal an increase in the frequency of butchery marks between Member 1 and Members 2–3 (Pickering et al., 2008). At the same time, however, while the absolute and proportionate numbers of bone tools are similar in Members 1 and 2, they are substantially more common in Member 3 (Brain and Shipman, 1993). Burnt bones that had been subjected to very high temperatures, such as engendered by campfires, have been recovered only from Member 3 (Brain and Sillen, 1988; Brain, 1993a). Thus, there are discernible differences among the archaeological records of the three members.

The taphonomy of Swartkrans has been the subject of intense investigation since the pioneering studies by Brain (1969, 1970, 1981, 1993c). Recent work that has contributed to our understanding of the complexities of these fossil accumulations has been undertaken by T.R. Pickering and colleagues (Pickering, 2001; Pickering et al., 2004, 2005, 2007, 2008). Brain provided convincing evidence that carnivores—specifically leopards—were responsible for the accumulation of the animal and hominin remains in Member 1, and he surmised that the bones in Member 2 also represent the prey items of leopards. However, he argued that there was a shift in Member 3 to greater hominin involvement in the accumulation of the faunal assemblage owing not only to the lower frequency of hominin remains therein, but also to the presence of butchered and especially burnt bones in that unit. Pickering et al. (2004, 2008) identified a clear predominance of leopard tooth marks on the bones—especially those of larger ungulates—in Member 1, confirming Brain's assessment, but they also found a notable increase in hyaena-sized dental pits on the bones in Members 2 and 3. Thus, they concluded that while leopards were the predominant accumulators of bones in Member 1, other carnivores may have contributed significantly to the Member 2 and

Member 3 assemblages. Pickering et al. (2008) argued that while hominins may have spent considerable time in the cave during the accumulation of Member 3, they were unlikely to have inhabited it during Member 1 and 2 times, endorsing Brain's (1981, 1993c) conclusion that the majority of hominin skeletal remains recovered from Swartkrans Members 1–3 were deposited by feeding carnivores.

### 3. The SKX 5013 hominin mandible

The SKX 5013 partial left mandibular corpus was discovered *in situ* by Brain during his excavation of the loose Member 2 deposit. The specimen (Fig. 1) contains an intact, worn M<sub>1</sub>. Most of the intact external surface of the bone reveals black discoloration, which also affects the dentine islands of the molar. However, the subsurface



**Figure 1.** The SKX 5013 left mandibular corpus in (a) occlusal, (b) lateral, and (c) lingual views. The lingual view was recorded following removal of the section of bone from the base of the mandible. Note the black MnO<sub>2</sub> staining that covers most of the external surface of the corpus, whereas the subsurface bone that has been exposed secondarily by subsequent spalling and fracture is free of stain. Scale bar in cm.

bone and the distal root of the P<sub>4</sub> that have been exposed secondarily by spalling and fracture are free of such pyrolusite (MnO<sub>2</sub>) staining. SKX 5013 was described by Grine (1989) and assigned by him to *P. robustus*. The cross-sectional properties of the corpus have been discussed by Daegling and Grine (1991) on the basis of CT scans recorded at the level of the M<sub>1</sub> and M<sub>2</sub>. The dense trabecular network in the postcanine corpus is comparable to that observed in other *P. robustus* jaws (Daegling and Grine, 1991; Grine and Daegling, 1993).

The apex of the socket of the M<sub>3</sub> mesial root appears fully formed with separate buccal and lingual radicular tips. This suggests that the root had completed development, which would be consistent with the M<sub>3</sub> having erupted prior to death. The jaw therefore derives from an adult individual.

The mandible is fairly small by comparison with other *P. robustus* jaws (Table 1; Fig. 2). As might be expected for a corpus of this size, the M<sub>1</sub> crown is also diminutive in relation to other *P. robustus* homologues (Table 2; Fig. 3). Although Schwartz and Tattersall (2003) have suggested that the SKX 4446 mandible, with which SKX 5013 agrees closely in size, is attributable to the genus *Homo*, their assignment has not withstood critical evaluation (Grine, 2005). Similarly, Thackeray et al. (2005) have opined that because the MD/BL crown shape indices of some of the smaller *P. robustus* M<sub>1</sub>s—including SKX 5013—overlap those of early *Homo* specimens, the former may represent males of the latter. However, pronouncements based on a single metric in which there is demonstrable overlap among species ranges are of little taxonomic utility (Scott and Lockwood, 2004; see also Gordon and Wood, 2013). Grine et al. (2012) have suggested a gorilla-like level of dimorphism in *P. robustus* on the basis of mandibular molar crown dimensions. If this holds, then SKX 5013 would most reasonably be regarded as a small adult female of this species.

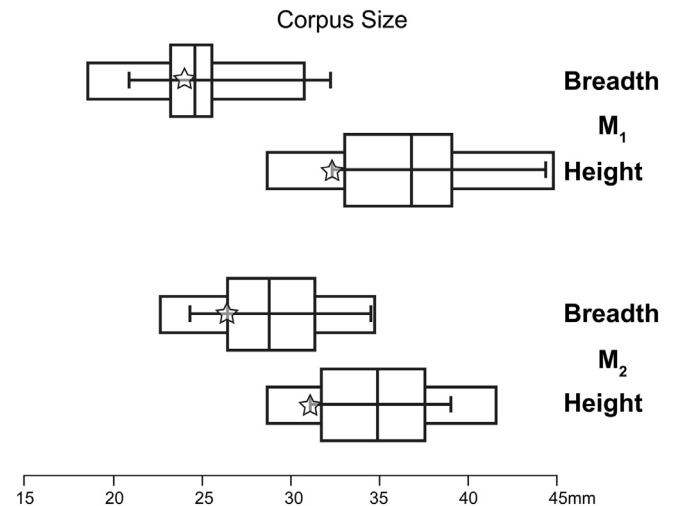
In 1988, a section of cortical bone was removed from the base of the corpus below the M<sub>1</sub> (Fig. 1c). The specimen was CT-scanned prior to removal of the bone section (see Daegling and Grine, 1991: Fig. 6). The slice at the base of the mandible measures 7.7 mm in height and 1.5 mm in thickness. The section was cut using a Buehler Isomet low-speed saw with a 0.3 mm thick series 15 HC diamond wafering blade. The loss of 0.6 mm of tissue to the mesial and distal cuts resulted in a bone section of 0.9 mm thickness.

The section of bone was removed from the inferior corpus to examine it for evidence of Haversian remodeling. Reflected light micrographs were published by Daegling and Grine (2007: Fig. 6.1), who noted that the section reveals a “strikingly low incidence of secondary osteons” representing only about 6% of the cortical bone area. Other mammal species that evince mandibular bone remodeling (e.g., canids and leporids) have much higher rates of bone turnover closer to the alveolus than at the base, suggesting that the low osteon population density in the basal part of the Swartkrans

**Table 1**  
Comparison of mandibular corpus breadth and height at the levels of the M<sub>1</sub> and M<sub>2</sub> in SKX 5013 and the *Paranthropus robustus* sample<sup>a</sup>.

Level	Dimension	n	mean	SE	SD	Obs. Range	
M <sub>1</sub>	Breadth	10	24.10	0.96	3.04	20.9–32.2	SKX 5013
			24.68				<i>P. robustus</i>
	Height	8	32.30	1.43	4.04	32.3–44.3	SKX 5013
			36.71				<i>P. robustus</i>
M <sub>2</sub>	Breadth	11	26.30	0.92	3.05	24.8–34.4	SKX 5013
			28.75				<i>P. robustus</i>
	Height	9	31.20	1.03	3.09	31.2–39.0	SKX 5013
			34.88				<i>P. robustus</i>

<sup>a</sup> The *P. robustus* sample comprises specimens from Swartkrans, Kromdraai, and Drimolen.



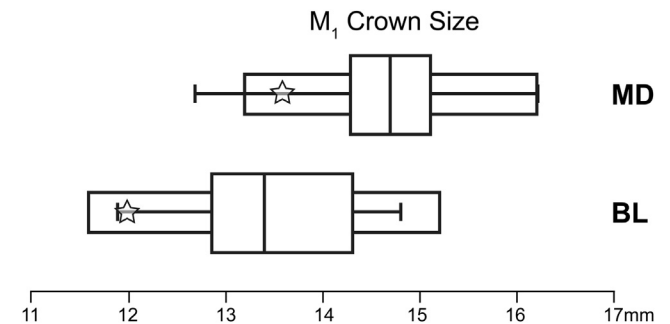
**Figure 2.** Box and whisker plots of the breadth and height of *Paranthropus robustus* mandibular corpora at the level of the M<sub>1</sub> and M<sub>2</sub>. The data used to construct these plots are recorded in Table 1. The open star indicates the position of SKX 5013. The tall rectangles encompass the lower and upper quartiles and contain the sample mean, the short rectangles indicate the fiducial limits of the sample, and the horizontal lines delineate the observed sample range.

**Table 2**  
Comparison of M<sub>1</sub> crown size in SKX 5013 and the *Paranthropus robustus* sample.<sup>a</sup>

	n	mean	SE	SD	Obs. Range	
MD	31	13.60	0.14	0.76	12.7–16.2	SKX 5013
		14.68				<i>P. robustus</i>
BL	28	12.00	0.17	0.88	11.9–14.8	SKX 5013
		13.44				<i>P. robustus</i>

<sup>a</sup> The *P. robustus* sample comprises specimens from Swartkrans, Kromdraai, and Drimolen.

jaw may not be unusual (Allen and Burr, 2008; Burr and Allen, 2009). On the other hand, osteonal bone densities in the mandibles of two species of Colobus monkey (*Procolobus badius* and *Colobus polykomos*) do not differ in the alveolar and basal regions, and the mandibular bone of a hard-food specialist, such as the sooty mangabey (*Cercocebus atys*) is not associated with elevated levels of osteonal remodeling (Daegling and McGraw, 2012). Given our limited knowledge of the extent of individual variation in mandibular Haversian remodeling among many primate (and especially hominoid) species, it is unclear what the low incidence of



**Figure 3.** Box and whisker plots of the MD and BL diameters of *Paranthropus robustus* M<sub>1</sub>s. The data used to construct these plots are recorded in Table 2. The open star indicates the position of SKX 5013. The tall rectangles encompass the lower and upper quartiles and contain the sample mean, the short rectangles indicate the fiducial limits of the sample, and the horizontal lines delineate the observed sample range.

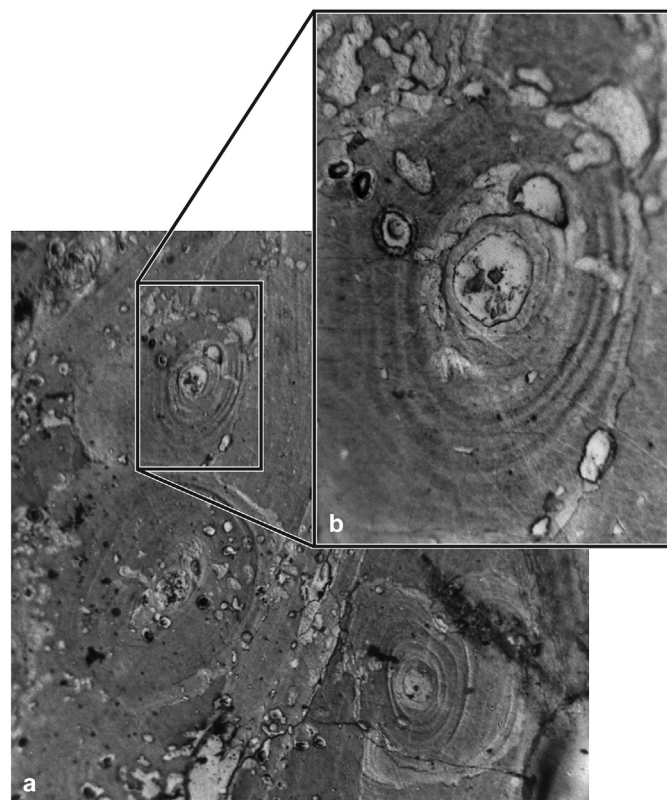
remodeling in this *P. robustus* jaw signifies. However, the observation of Haversian remodeling in this specimen does not appear to have been compromised by MFD.

#### 4. Evidence of microbial osteolysis in SKX 5013

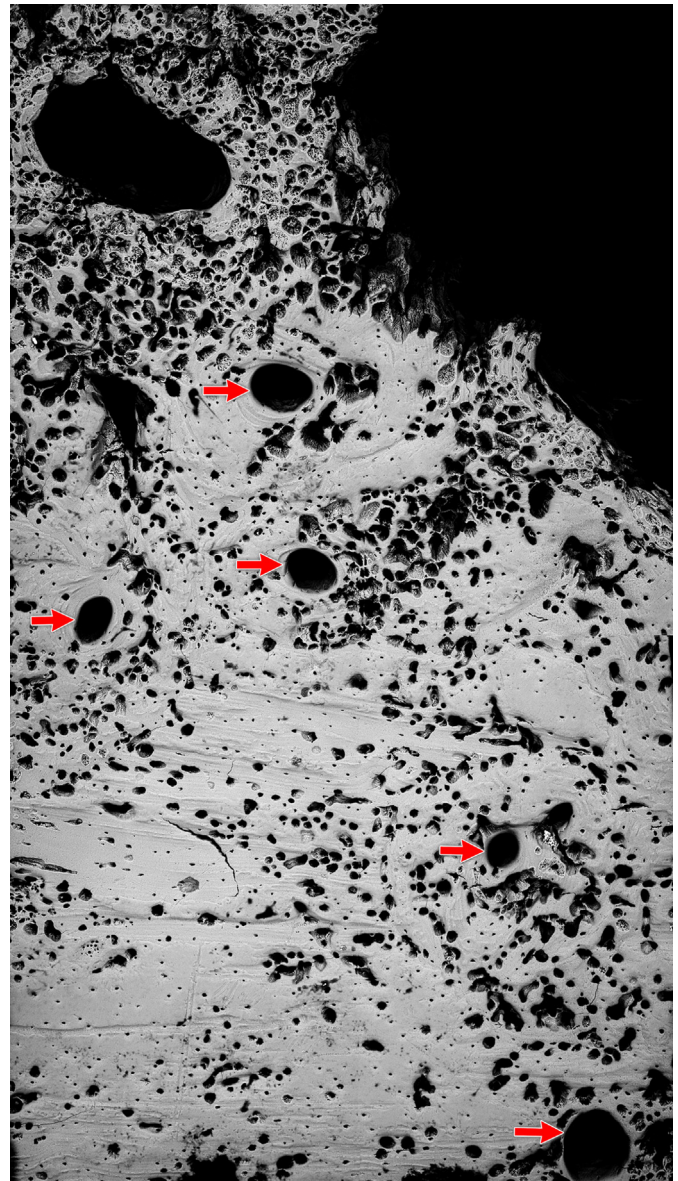
In their discussion of the images obtained from the section of the SKX 5013 mandible, Daegling and Grine (2007: 85) made note of “irregular bubbles” that occur throughout, referring to them as “inclusions of an unspecified nature.” The reflected light micrographs to which Daegling and Grine (2007) referred are reproduced here in Figure 4.

The entire section was examined by backscattered electron microscopy in a scanning electron microscope (BSE-SEM) using a Zeiss EVO 50 (8.5 mm working distance, 15 kV accelerating voltage, 600 pA beam current, and 100 Pa pressure). BSE-SEM imaging reveals numerous small cavities across the section. However, these features tend to be concentrated around Haversian canals, and they are much more abundant closer to the endosteal aspect of the section (Fig. 5). The appearance and distribution of the cavities are consistent with non-Wedl MFD, which commonly occur around vascular canals (Turner-Walker et al., 2002).

The MFD can clearly be differentiated from the osteocyte lacunae (Fig. 6) and appear as irregular resorption cavities with spongiform walls (Fig. 7). Moreover, the BSE-SEM images reveal that many of the MFD have hypermineralized rims, where the white coloration indicates higher density bone than the surrounding matrix (Fig. 7). This is due to dissolution of the bone



**Figure 4.** Reflected light micrographs of Haversian bone in the inferior corpus of the SKW 5013 *Paranthropus robustus* mandible from Swartkrans. (a) Micrograph showing three osteons surrounding central Haversian canals. (b) Enlargement of the osteon in the upper left corner of (a) showing concentric lamellae. The irregular “bubbles” are inclusions of an unspecified nature. Illustration and caption taken from Daegling and Grine (2007: Fig. 6.1).

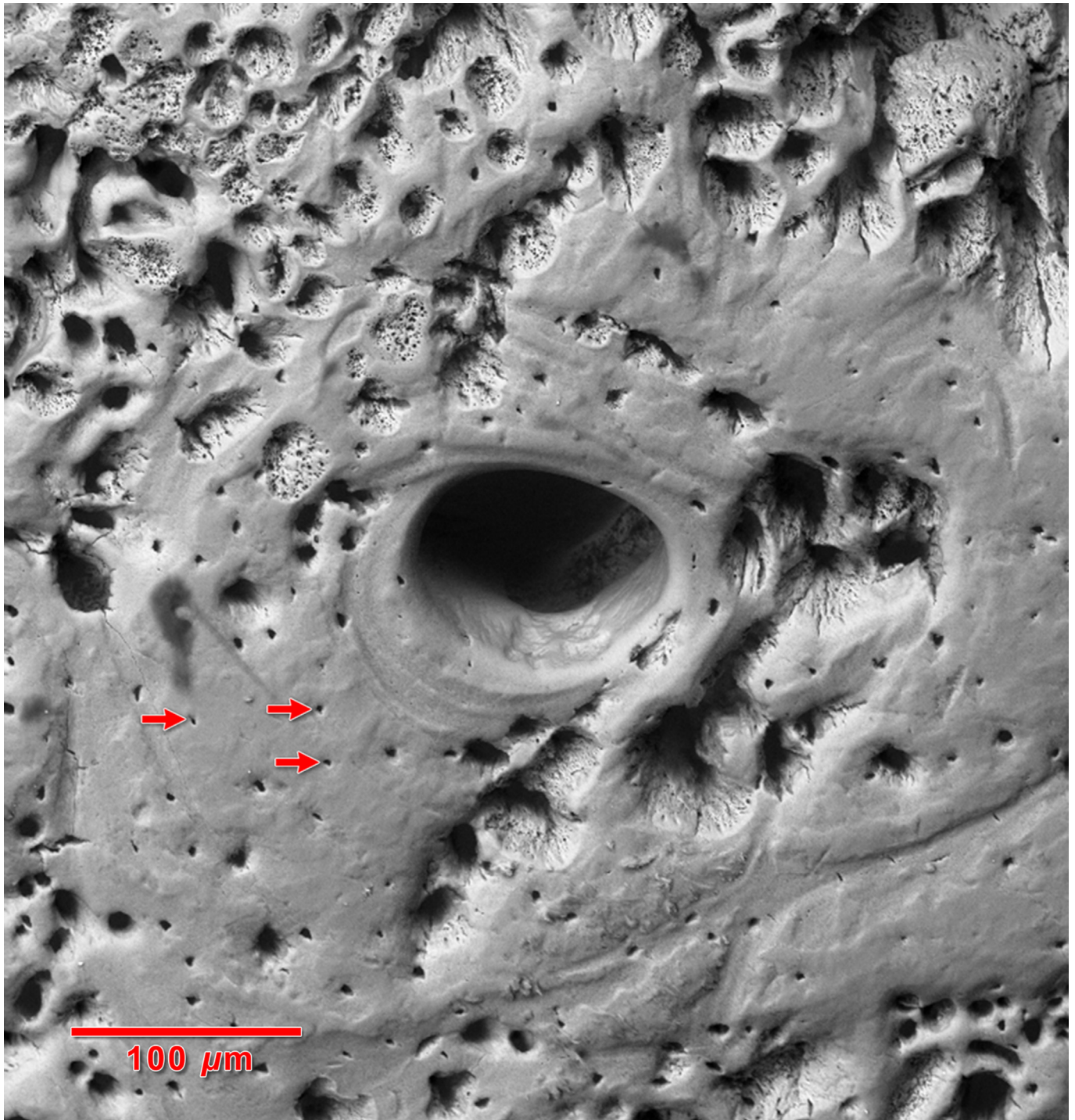


**Figure 5.** Backscattered scanning electron micrograph of a portion of the section of cortical bone removed from the SKX 5013 mandible. A number of Haversian canals (indicated by arrows) are clearly identifiable. The periosteal aspect of the section is towards the bottom of the micrograph; lingual side of the section is to the right. Note that the MFD tend to be concentrated around the Haversian canals and are especially numerous closer to the endosteal aspect of the section, which is at the upper right. Field width = 1.4 mm.

mineral phase by bacterial lysis and the re-precipitation of the mineral ions against the walls of the MFD and the small spaces internal to these pits.

According to the types of MFD defined by Hackett (1981), the resorption lacunae that dominate the section would be characterized predominantly as linear longitudinal and budded tunneling. The MFD cavities observed in this section clearly resemble the type of evidence for microbial attack that has been documented in archaeological bone (Bell, 1990; Hedges et al., 1995; Jackes et al., 2001; Turner-Walker and Syversen, 2002; Turner-Walker et al., 2002; Jans et al., 2004; Fernández-Jalvo et al., 2010).

The extent of MFD in this specimen is also clearly visualized by microradiography (Fig. 8). Examination of the microradiographs and the lower magnification BSE micrographs (e.g., Fig. 5) suggests

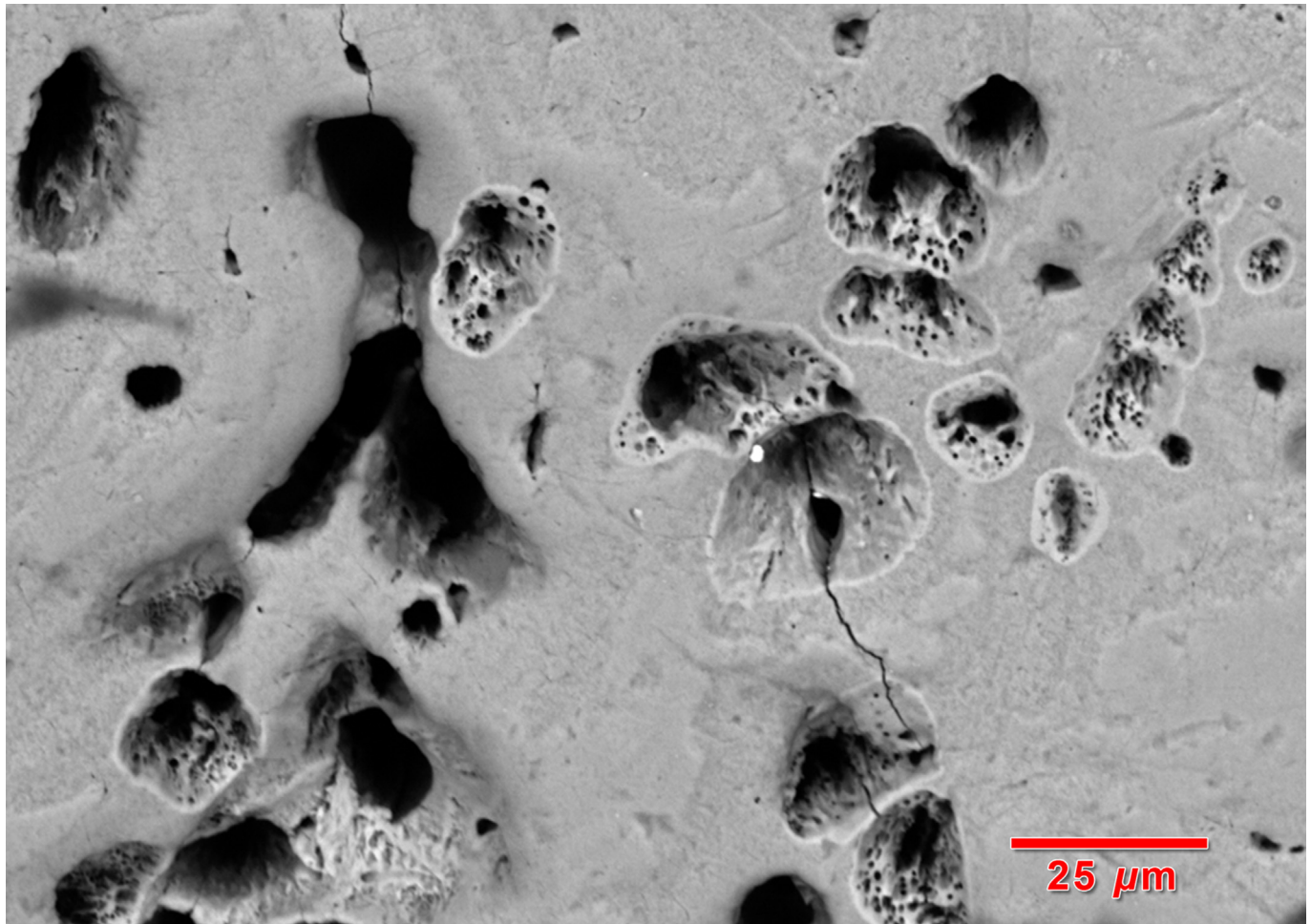


**Figure 6.** Backscattered scanning electron micrograph of cortical bone from the inferior aspect of the SKX 5013 mandible. The Haversian canal shown here is the uppermost of those indicated with arrows in Figure 5. Note the numerous linear longitudinal and larger budded MFD can easily be distinguished from the osteocyte lacunae (indicated by arrows).

that the degree of MFD in this fossil most closely approximates an Oxford Histological Index (OHI) value of 3 as defined by Hedges et al. (1995; also see Millard, 2001: Table 5.1). Specimens categorized as OHI 3 reveal clear preservation of some osteocyte lacunae with approximately 67% of bone preserved intact.

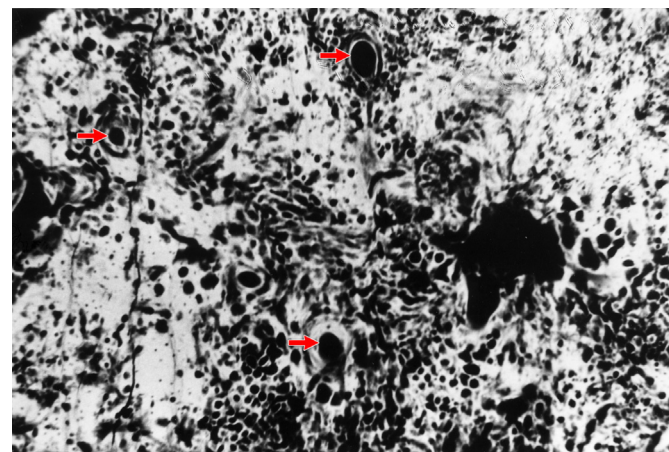
There is little, if any evidence in this small section of Type 1 Wedl branching tunnels. As noted above, these occur principally along the periosteal margins of bones and are held to be produced by fungi and cyanobacteria (Turner-Walker et al., 2002). The black discoloration that affects the external surfaces of the corpus and

dentine islands on the molar of SKX 5013 is of potential relevance in this regard because of the mechanisms that have been posited to underlie such pyrolusite ( $\text{MnO}_2$ ) staining. The dolomitic bedrock into which the karst cavities were formed has a consistent MnO content of about 0.3% (Truswell and Eriksson, 1975), which is released on dissolution to form pyrolusite in the soils that infill the karst features. Secondary dissolution (decalcification) of the consolidated sediments through the development of “Makondos” releases the manganese that has been entrapped by the calcite lattices to enable the black staining that is a common feature on the



**Figure 7.** Backscattered scanning electron micrograph of cortical bone from the inferior aspect of the SKX 5013 mandible. Note the submicron porosities that constitute the spongiform walls of the MFD cavities. Note also that many of the MFD cavities exhibit hypermineralized rims. This image is higher magnification of the region around the Haversian canal in the upper left of Figure 5.

bones from these and other palaeokarst caves (Potter and Rossman, 1979; Brink and Partridge, 1980; Hill, 1982). Manganese oxidation can also result from the activity of soil bacteria such as *Anthrobacter*, which accumulates  $MnO_2$  in its sheaths and filaments (Paul and Clark, 1989; Tebo et al., 2005). As such, the origin of the



**Figure 8.** Microradiograph of cortical bone from the inferior aspect of the SKX 5013 mandible. A small number of Haversian canals (several are indicated by arrows) are only just identifiable among the numerous MFD cavities. Field width = 2.3 mm.

manganese staining may be due to biodegradation in the sediment (López-González et al., 2006; Marín-Arroyo et al., 2008, 2014).

Nevertheless, even if exogenous soil bacteria were responsible for the  $MnO_2$  staining of this fossil jaw fragment, it is clear that this is restricted to the external-most aspect of bone, with the subsurface bone that has been exposed secondarily by spalling and fracture being free of this black discoloration. This observation is consistent with the finding of Kuczumowa et al. (2010: 114), who showed that the manganese stain penetrates to a depth of only about 250  $\mu m$  on fossil bones from the South African palaeokarst caves and concluded that it appears *not* to have “influenced the organic material in the bulk bone.” Indeed, they suggested that the  $MnO_2$  formed a “very efficient protective layer” against further intrusion by organic matter from the outside.

Finally, the MFD that is evident in the cortical bone of the *Paranthropus* jaw is almost certainly not the result of gastric acid etching by large-bodied carnivores, as the specimen displays none of the characteristic features of partially digested and regurgitated elements (Horwitz, 1990; Grupe, 2007). In particular, the external surface of the bone and the exposed tooth enamel is free of corrosion and the fractured bone margins are sharp.

##### 5. Microbial attack and Swartkrans taphonomy

Microbial erosion of bone can begin very soon after death (within days), and complete destruction can also be accomplished



in a relatively short interval (Hedges and Milliard, 1995; Bell et al., 1996; Jans, 2008). The histological features of bone that are related to microbial lysis may potentially assist in the reconstruction of the taphonomic history or “diagenetic trajectory” of a single specimen or even an assemblage of specimens (Bell et al., 1996; Turner-Walker and Jans, 2008; Turner-Walker, 2012). Observations of intact human skeletons compared to disarticulated and fragmented (i.e., butchered) animal bones from archaeological sites have supported a model of primary endogenous bacterial responsibility (Bell et al., 1996; Nielsen-Marsh and Hedges, 2000; Jans et al., 2004; Nielsen-March et al., 2007; Smith et al., 2007; White and Booth, 2014).

As such, the state of microbial osteolysis in the SKX 5013 mandible and its preferential distribution both endosteally and in association with Haversian canals suggest that this particular *P. robustus* individual may well have remained at least partially intact after death, and that putrefaction set in with gut microbes being distributed into the vascular system prior to fragmentation of the skull. Of potential interest in this regard is the observation that the largest concentrations of MFD are typically to the lingual side of and somewhat below the vascular (Haversian) canals, which may reflect the orientation of the bone while it was undergoing microbial osteolysis. Of course, the manner by which death occurred, and where death and putrefaction took place are wholly unknown and almost certainly will remain so.

While these observations on bioerosion provide a glimpse into the taphonomic history of this particular presumptive female australopithecine, they are silent about the rest of the Member 2 hominin assemblage, and they do not speak at all to the associated faunal assemblage. However, given the possibility that different agents of accumulation may have been responsible for the faunal and hominin fossils in the three earliest members at Swartkrans (Brain, 1969, 1970, 1981, 1993c; Pickering, 2001; Pickering et al., 2004, 2005, 2007, 2008), it is of potential interest that a hominin fossil from Member 2 displays significant microbial osteolysis.

Of course, a number of unresolved and potentially confounding issues such as the moisture history and chemistry of the soil into which the remains were deposited, and their location within the cave itself, caution against overly simplified taphonomic interpretations. Nevertheless, a study of the prevalence of microbial osteolysis in adequately large samples of the numerous animal bones from these units may yield novel insights and provide refinement of our understanding of their taphonomic histories. It is conceivable that such observations might well reveal differences among the various members that could provide another valuable source of osteoarchaeological information at the site of Swartkrans.

## 6. Conclusions

Microbiological degradation is one of the most important factors responsible for the destruction of bone in archaeological contexts. Microscopic focal destruction (MFD) is the most prevalent form of microbial tunneling and is encountered very commonly in human bones from archaeological sites, whereas animal bones from these same sites show significantly better preservation if they were deposited in a fragmentary (e.g., butchered) state. These observations together with experimental evidence point to an endogenous origin for osteolytic bacteria, which suggests that bone bioerosion could potentially aid in reconstructing early taphonomic events. We here report extensive MFD in the mandibular corpus of a small (presumptive female) individual of the hominin *P. robustus* from the Early Pleistocene site of Swartkrans, South Africa. The specimen (SKX 5013) derives *in situ* from the Member 2 deposit, which is dated to ca. 1.5–1.0 Ma. Examination of sections from the corpus by

BSE-SEM microscopy reveals numerous small, linear longitudinal and budded tunneling cavities, which tend to be concentrated around Haversian canals and are more abundant closer to the endosteal aspect of the section.

The taphonomy of Swartkrans has been the subject of intense investigation, and given the possibility that different agents of accumulation may have been responsible for the faunal and hominin fossils in the different members at the site, the observation that a specimen of *P. robustus* from Member 2 displays significant microbial osteolysis may be of potential interest. Analyses of the incidence of microbial osteolysis among the faunal remains from these units may serve to further elucidate their taphonomic histories, thus providing an additional source of information relating to the site formation processes at Swartkrans.

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