Characterization of bone surface modifications on an Early to Middle Pleistocene bird assemblage from Mata Menge (Flores, Indonesia) using multifocus and confocal microscopy

Hanneke J.M. Meijer[a,b,*], Francesco d'Errico[c,d], Alain Queffelec[c], Iwan Kurniawan[e], Erick Setiabudi[e], Indra Sutisna[e], Adam Brumm[f], Gerrit D. van den Bergh[g]

[a] University Museum of Bergen, Department of Natural History, University of Bergen, Postbox 7800, 5020 Bergen, Norway
[b] Human Origins Program, Department of Anthropology, National Museum of Natural History, Smithsonian Institution, Washington, DC, United States of America
[c] Centre National de la Recherche Scientifique, UMR 5199 –PACEA, Université de Bordeaux, Pessac CEDEX, France
[d] SFF Centre for Early Sapiens Behaviour (SapienCE), University of Bergen, Norway
[e] Geology Museum, Bandung 40122, Indonesia
[f] Australian Research Centre for Human Evolution, Environmental Futures Research Institute, Griffith University, Brisbane, Queensland 4111, Australia
[g] Centre for Archaeological Science, School of Earth & Environmental Sciences, University of Wollongong, Wollongong, New South Wales 2522, Australia

ARTICLE INFO

ABSTRACT

Island Southeast Asia (ISEA) is a key region for the study of human evolution. New fossil and archaeological evidence, from several islands, suggests an Early to Middle Pleistocene colonisation date by hominins. A taphonomic framework, however, such as that exists for Africa, is currently lacking, and taphonomical studies of ISEA vertebrate assemblages are very limited. In this paper, we apply multifocus and confocal microscopy to surface modifications on an Early to Middle Pleistocene avian assemblage from Mata Menge, in the So'a Basin of central Flores, Indonesia, with the aim of characterizing material and testing the relevance of 3D reconstructions to study the taphonomy of ISEA bone assemblages. Our observations document a number of bone surface modifications, including individual parallel grooves, overlapping spindle-like striations, elongated impacts, short composite grooves, and rows of pits. These features suggest that several taphonomic agents were at play during and after the accumulation of the Mata Menge small vertebrate assemblage. We find no unambiguous evidence for the exploitation of birds by the So'a Basin hominins, or for hominins being a significant accumulating agent of avian remains at Mata Menge. However, our work should be seen as preliminary, as direct comparative data on relevant biological agents are lacking. The markedly distinct faunal composition and climatic regimes of many Southeast Asian islands, and the potential use of different tools by hominins, warrants the development of a comprehensive taphonomical framework that is specifically relevant for ISEA.

1. Introduction

The late Early to early Middle Pleistocene (1.0–0.7 Ma) fossil-bearing localities in the So'a Basin (Fig. 1) of central Flores, Indonesia, contain the earliest evidence for hominins in Wallacea (van den Bergh et al., 2016). The Dutch priest and archaeologist Theo Verhoeven was the first Western observer to discover and report stone tools associated with fossils of the extinct elephant *Stegodon* near Mengeruda in the So'a Basin in central Flores (Maringer and Verhoeven, 1970). However, it took until 2014 before the first hominin remains were discovered at the early Middle Pleistocene So'a Basin site Mata Menge. The fossil remains – isolated adult and infant teeth and a mandible fragment – indicate a small hominin species very similar, and probably ancestral, to *Homo floresiensis*, known from the Late Pleistocene deposits at Liang Bua, 74 km northwest of the So'a Basin (van den Bergh et al., 2016; Brumm et al., 2016).

To date, over 28,000 faunal remains have been excavated from two superimposed stratigraphic fossil-bearing beds, or intervals, at Mata Menge, both reflecting the same impoverished, insular fauna consisting of the intermediate-sized proboscidean *Stegodon florensis*, a giant rat *Hooijeromys nusatenggara*, Komodo dragons *Varanus komodoensis*, crocodiles, birds, frogs, and freshwater gastropods (Meijer et al., 2015; Brumm et al., 2016). So far, all hominin fossils were found in the upper fossil-bearing interval in a single fluvial sandy layer. Several lines of
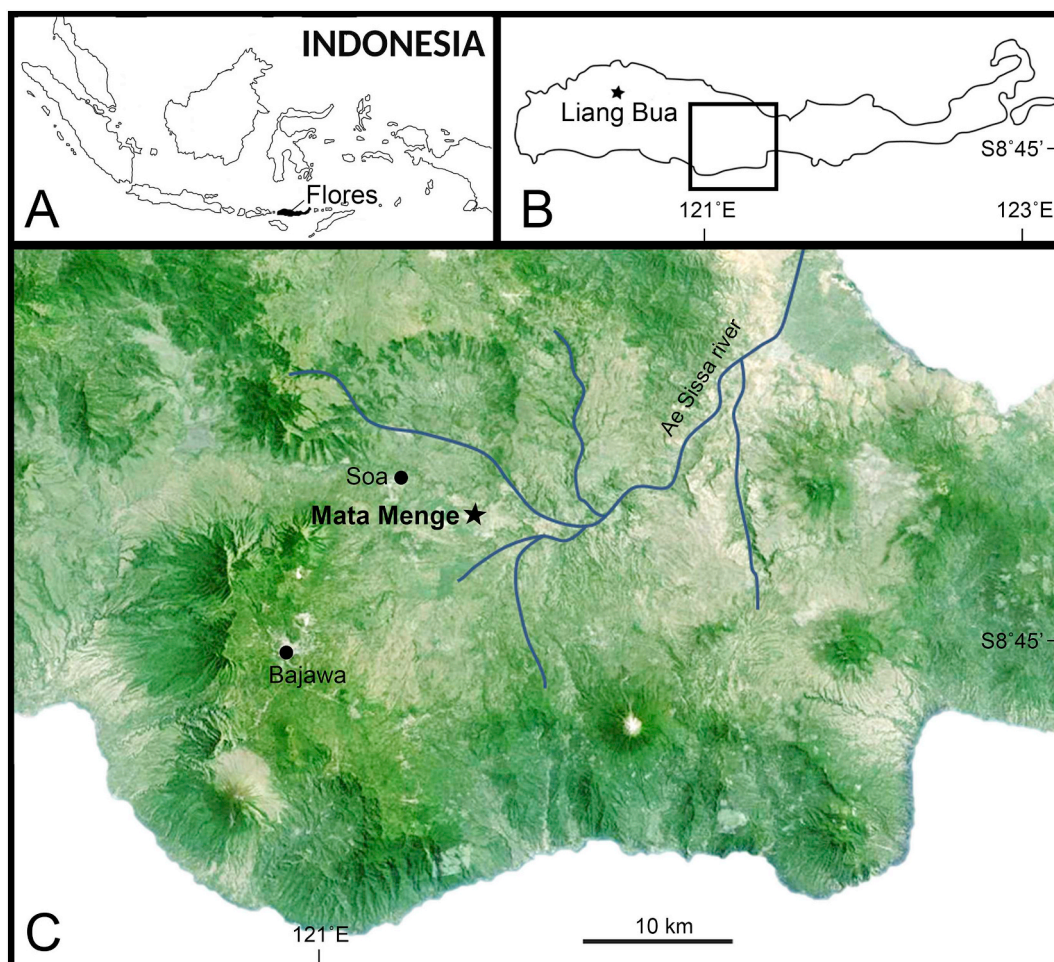
Fig. 1. Location of study site. (A) Position of Flores in Southeast Asia; (B) map of Flores with location of the studied region enlarged in C shown by box; (C) aerial view (source: Google Earth). Location of central Flores, the Mata Menge site in the So'a Basin and the location of Flores.

palaeoenvironmental evidence suggest that the Mata Menge hominins inhabited a savannah-like tropical grassland habitat with a wetland component (Brumm et al., 2016). In both levels the faunal remains are directly associated with stone artifacts, although it is not clear if any stone tools were used in processing faunal remains (Brumm et al., 2016). The lithic assemblage reflects a technologically straightforward core-and-flake approach to stoneworking. Notably, the Mata Menge assemblage is technologically similar to the stone artifacts from Late Pleistocene sediments at Liang Bua associated with *H. floresiensis* (Brumm et al., 2006; Moore et al., 2009; Brumm et al., 2016). The persistence of this technology over hundreds of millennia on Flores is noteworthy. To date, no anthropogenic marks have been identified on the Mata Menge faunal remains, and it is unknown to what degree, if at all, the hominins contributed to the accumulation of the Mata Menge faunal assemblage.

Despite renewed scientific interest in Island Southeast Asia (ISEA) as a focal point for the study of human evolution, a taphonomic framework, such as that exists for Africa (Behrensmeyer, 1978; Brain, 1981; Blumenschine, 1989; Domínguez-Rodrigo et al., 2007; Pickering et al., 2007; Sahle et al., 2017), is lacking. Open air sites such as the Sangiran dome on Java and the So'a Basin on Flores have yielded some of the earliest known vertebrate remains, including evidence for hominins, in the region, yet taphonomical studies on these assemblages are very limited and often preliminary in nature (Bouteaux et al., 2007; van den Bergh et al., 2009, 2014). Aspects of cave taphonomy and site formation processes have been discussed for Liang Bua on Flores (Morley et al., 2017; Sutikna et al., 2018; Veatch et al., 2019), Laili Cave on

Timor (Hawkins et al., 2017) and Tron Bon Lei on Alor (Hawkins et al., 2018). A systematic review of the processes involved in the accumulation of vertebrate remains in Southeast Asian cave environments (Louys et al., 2017) suggests that biological agents are the dominant accumulators of vertebrate remains. Clear differences exist between caves on islands east and west of the Wallace Line, as Wallacean islands typically lack mammalian carnivores and other mammals that can act as taphonomic agents, such as porcupines. Bone accumulations in Southeast Asian caves therefore mainly result from the actions of owls and modern humans (Louys et al., 2017). Evidence for a potential role of premodern humans in accumulating vertebrate remains is almost non-existent. Bouteaux and Moigne (2010) report on the presence of cut marks on artiodactyle (*Axis* and *Duboisia*) long bones as well as intentional breakage of long bones at the Middle Pleistocene site of Ngebung 2 in the Sangiran Dome on Java. At an early Middle Pleistocene site in the Cagayan Valley on Luzon, cut marks and impact marks on bones of a partially preserved rhino skeleton also point to intentional hominin interference with faunal remains (Ingicco et al., 2018). The exploitation of shellfish as tools by *Homo erectus* in the Middle Pleistocene of Java (Choi and Driwantoro, 2007; Joordens et al., 2015) and the potential reliance of hominins on bamboo technology (West and Louys, 2007) should be considered when looking for potential anthropogenic bone surface modifications.

Understanding the biogeography of Flores, an oceanic island, is essential in interpreting the role of biological agents in accumulating bone assemblages. Prior to the Neolithic, *Stegodon* was the only large herbivore, and mammalian carnivores, such as hyenas and big cats,

were absent (van den Bergh et al., 2009). The only predators, and thus potential accumulators, of bone assemblages were crocodiles, Komodo dragons (Brumm et al., 2016), and hominins. Although (giant) rats are unlikely to have acted as accumulating agents, they are known to modify bone surfaces (see Meijer et al., 2013 for examples from Liang Bua). Avian predators, such as the eagle owl *Bubo* sp. and the eagle *Aquila* sp. (Meijer et al., 2015) may have contributed small vertebrates to the faunal assemblages. Crocodiles have only recently been recognized as taphonomic agents (Njau and Blumenschine, 2006). The role of Komodo dragons as accumulators of vertebrate bone assemblages is unclear. Brumm et al. (2016) hypothesize that the Mata Menge artifacts and faunal remains from the upper fossil-bearing interval, including hominin elements, were transported short distances by the stream that deposited the fossil layer, before mudflows originating from within the Welas Caldera inundated the stream valleys with meter-thick muddy debris. A preliminary taphonomic study of a sub-sample of *Stegodon* dental remains from the lower fossil-bearing interval (van den van den Bergh et al., 2014) indicates that the *Stegodon* assemblage corresponds with that of a living population, in agreement with a catastrophic scenario, most likely associated with volcanic activity. Although the possibility that hominins contributed to the accumulation of fossil *Stegodon* remains at Mata Menge cannot be ruled out, these findings suggests that it was unlikely, despite the juxtaposition of stone artifacts and *Stegodon* remains. To better understand the factors that lead to the accumulation and preservation of the remains of hominins and other vertebrates in the So'a Basin, it is necessary to identify the taphonomical agents and processes at work and evaluate their roles in the formation of the So'a Basin fossil deposits. This entails distinguishing bone surface modifications made by anthropogenic from non-anthropogenic agents.

3D reconstructions of bone surface modifications are increasingly used in taphonomic studies and the last few years have witnessed a rapid growth of works in which quantification of the internal morphology of marks produced by known agents is used to identify diagnostic criteria to be applied to the taphonomic interpretation of bone assemblages. Most of these studies were devoted to distinguish carnivore modifications (for instance see Harris et al., 2017; Pante et al., 2017; Sahle et al., 2017; Yravedra et al., 2018), weathering (Vietti, 2016) and fluvial abrasion (Gümrükçü and Pante, 2018) from cut marks, or to identify the raw material and type of stone tools used in butchering activities (e.g. Courtenay et al., 2017, 2018; Yravedra et al., 2017; Otárola-Castillo et al., 2018).

Early and Middle Pleistocene bone accumulations from Africa and, to a lesser extent, from Europe, have been the main focus of these studies. Thus far, none of these investigations has addressed modifications produced by taphonomic agents on avian remains nor on bone assemblages from Southeast Asian sites; however given the differential faunal composition of many Southeast Asian islands, potential use of different tools, as well as differences in climatic regimes and volcanic activity (active explosive volcanism with periodic cycles of large sediment generation followed by volcanic quiescence with subsequent erosion of sediments), knowledge of taphonomic agents and processes derived from African and European sites may not be directly applicable to bone assemblages from Southeast Asia.

Here we apply multifocus and confocal microscopy to surface modifications on avian remains from Mata Menge with the aim of characterizing them and testing the pertinence of 3D reconstructions to study the taphonomy of Southeast Asian insular bone assemblages.

2. Methodology

2.1. Geological setting

The So'a Basin is an extensive (~400 km^2) sedimentary depression located northwest of Bajawa, the capital of the Ngadha Regency of central Flores (Fig. 1). The basin is surrounded by active and non-active

volcanoes and is drained by the Ae Sissa River to the northeast. The ~100 m thick Ola Kile Formation (OKF) comprises the basement unit and is predominantly composed of massive volcanic breccias associated with a former volcanic centre, the Welas Caldera, and deposited in the Late Pliocene/Early Pleistocene. The Ola Bula Formation (OBF) unconformably lies on top of the OKF. Three members can be distinguished within the OBF. The basal member is dominated by white and pink pumice tuffs that were mostly deposited as ignimbrites and laharic mudflows, but also include fall-out tephras. On top of this lies a sandstone member characterized by an alternation of fluvial sandstones, mudflows, and fluvio-lacustrine siltstones, indicative of a predominantly fluvial environment. Both the tuff and sandstone members have yielded vertebrate fossils remains, but avian remains are so far restricted to the sandstone member. A lacustrine limestone sequence caps the sandstone layers (Suminto et al., 2009; Brumm et al., 2016). All localities have yielded remains of highly insular endemic faunas, but hominin remains are thus far only known from the upper fossil-bearing level of the sandstone member at Mata Menge (van den Bergh et al., 2016). An additional 15 terrestrial fossil localities have yielded proxy evidence for hominins (i.e., stone artifacts). The oldest known fossil locality in the basin, Tangi Talo, appears to pre-date the arrival of hominins on the island (Aziz et al., 2009) and contains no stone artifacts or other signs of a hominin presence.

The site of Mata Menge is located near the northwestern margin of the So'a Basin (Fig. 1). Large-scale excavations here over multiple field seasons (1992–1998, 2004–2006, and 2010–2015) have produced the remains of an insular fauna (van den Bergh et al., 2009; Brumm et al., 2016) along with an abundance of flaked stone artifacts (Brumm et al., 2009; Brumm et al., 2016). Mata Menge exposes two main fossil-bearing intervals (Brumm et al., 2016, Fig. 1). The lower fossil-bearing interval, exposed in trenches 1–8 and 11–31D, is 1.6–2.2 m thick and comprises interbedded layers and lenses of tuffaceous siltstone and sandstone, indicative of a lakeshore setting close to a tributary stream (van den Bergh et al., 2009). The vertebrate fossil and artifact-bearing layers are bracketed by two zircon fission-track ages with a maximum age of 0.88 ± 0.07 Ma and a minimum age of 0.80 ± 0.07 Ma (Morwood et al., 1998; O'Sullivan et al., 2001). The upper fossil-bearing interval (Layer II) is exposed in trenches 12 and 32 (Brumm et al., 2016), and contains hominin fossils in addition to vertebrate fossils and artifacts (van den Bergh et al., 2016). Layer II is a less than 30-cm-thick sandstone and represents the deposit of a small, sinuous stream tributary. Multiple dating methods suggest an age of 0.7 Ma for Layer II (Brumm et al., 2016).

2.2. Methods and taphonomic analysis

The avian remains from Mata Menge stem from the 2004–2006 and 2010–2015 field campaigns and are stored at the Geology Museum in Bandung. The fossils were excavated with the help of local community members supervised by a team of Indonesian and Australian researchers. Due to the nature of the sedimentary matrix, which generally consists of hard, concrete-like sandstone, we used small metal hand tools (e.g. fine chisels and nails) to carefully excavate the fossils. Finds were largely exposed or directly bagged and left in their original position until their 3D coordinates were recorded with a total station (Brumm et al., 2016). During plotting with the TS, finds were numbered and labelled. Fossils with cracking or other surface damage were impregnated with a hardening solution (Paraloid) prior to further treatment. To prevent possible damage, large or fragile fossils were covered with a plaster jacket prior to lifting and transport. Preliminary taxonomic identification of fossils was performed at the basecamp, after which individual finds were packed in crates and transported to the laboratory at the Geology Museum in Bandung for further cleaning and analysis.

Avian remains were identified further using the avian skeleton collections at the Smithsonian Institution's National Museum of Natural

History (NMNH) in Washington, DC (USA), the Natural History Museum (NHM) at Tring (UK), and the Senckenberg Museum and Forschungsinstitut (SMF) in Frankfurt (Germany) (Meijer et al., 2015; Brumm et al., 2016). The fossils were first examined with a 10× hand lens under oblique light to detect bone surface modifications at the Geology Museum in Bandung. The taphonomic analysis of bird remains entailed recording the following taphonomic parameters: completeness, cracking, flaking, surface dissolution, color, presence/absence of manganese deposits, and presence/absence of marks, including root marks, trampling marks, and any marks indicative of probable carnivore and rodent activity, as well as possible anthropogenic modifications. A subset of twenty bones was selected for further analysis at the PACEA laboratory in Bordeaux, and permission was obtained to export this material. The selected bones were examined with a motorised Leica Z6APOA microscope equipped with a DFC420 digital camera and Leica Application Suite (LAS) software, including the Multifocus module and Leica Map DCM 3D software. The Multifocus module permits the acquisition of extended depth of field images by relying on adapted algorithms that combine digital images collected at different heights into a single, sharp, composite image. The obtained microscopic images were digitized and edited in the Adobe® Photoshop® CS5.1 Extended software. The Leica Map DCM 3D allowed production of 3D reconstructions of areas of interest.

High-resolution surface topography was acquired with a Sensofar S neox confocal microscope driven by SensoScan 6 software (Sensofar, Barcelona). Two different objectives were used for 3D reconstruction and imaging. A 20× objective allowed for 0.69 μm and 0.31 μm lateral and vertical resolution respectively. In addition, a long-working distance 50× objective allowed for 0.28 μm and 0.17 μm in lateral and vertical resolution.

3. Results

3.1. General taphonomy

The 2004–2006 and 2011–2015 field campaigns at Mata Menge yielded 187 avian remains (Table 1). Eight specimens were too small or too coated with hardened sediment to record any meaningful information. The assemblage contains at least nine taxa including Anatidae (*Cygnus* sp., *Anas* cf. *gibberifrons*, cf. *Tadorna*), Accipitridae (cf. *Hieraaetus*), Rallidae (cf. *Gallinula/Fulica*), Charadriidae (*Vanellus* sp.), and Passeriformes (Meijer et al., 2015). Most specimens come from the upper fossil-bearing interval in Trench 32 (*n* = 66), which also yielded the hominin fossils. One hundred and forty-one specimens (79%) showed longitudinal cracking of the bone surface, but only twenty-four (13%) showed any signs of flaking. Sixty-five specimens (36%) show surface dissolution. Ninety-six specimens (54%) show manganese staining, but the degree of staining varies significantly and ranges from a few patches to extensive mottling of the bones.

Table 1

Number of identifiable specimens (NISP) and taphonomic data for Mata Menge in total and for each of the four main excavation trenches (E-23, E-27, E-31 and E-32).

	Interval[a]	*n*[b]	Cracking	Flaking	Dissolution	Manganese
Total		179	141	24	65	96
E-32	Upper	66	50	5	19	31
E-23	Lower	20	17	3	5	11
E-27	Lower	53	40	7	27	28
E-31	Lower	13	11	4	4	10

[a] Interval refers to the lower and upper fossil intervals at Mata Menge (see Section 2.1).

[b] *n* indicates the number of specimens for which taphonomical data could be recorded, and the number of specimens displaying cracking, flaking, dissolution marks, and manganese staining.

3.2. Surface modifications

Multifocus and confocal microscopy identified five categories of marks (Table 2): parallel grooves, overlapping spindle-like striations, short and superficial composite grooves, elongated impacts, rows of pits, and etch pits.

3.2.1. Individual parallel grooves

A left proximal anatid radius from Trench 30B (F.166) displays seven linear, parallel grooves on the ventral surface of the proximal half of the shaft (Fig. 2). The grooves are straight and oriented transversely with regard to the long axis of the shaft (Fig. 2A–B). They measure 20–40 μm in width and are up to 1 mm long. Internal striations are clearly visible inside the grooves, which appear remarkably well preserved. 3D imaging (Fig. 2E–F) shows that they are shallow (~10 μm), relatively wide, and feature an asymmetric V-shaped cross-section. The bone surface displays several long cracks that run parallel to the long axis of the bone and that are filled with dark sediments, indicating that these cracks are ancient (a number of bones show recent cracks that are light in color and do not appear to contain sediment). Five out of the seven marks run across one of these cracks. SEM (details in Fig. 2B) and confocal imaging show that the grooves' internal striations are fresh and not interrupted by the crack, but extend over the sediment filling the crack. Furthermore, close examination of the grooves reveals the presence of dark sediment particles originating from the crack that lay at the bottom of the marks. They appear to have been displaced by the taphonomic agent responsible for the grooves. This phenomenon, which is observed in all the marks that cross the crack, suggests that the grooves postdate the formation of the crack.

3.2.2. Overlapping spindle-like striations

Thin, elongated, randomly oriented spindle-like striations occur on a number of bone fragments. A good example of these marks is seen on F.2802, a distal radius of a swan (*Cygnus* sp.) from Trench 27B (Fig. 3A). These marks are not limited to certain areas of the bone but occur all over the bone surface. On F.2802 (Fig. 3), two different types of striations are recorded. There are individual, short striations as well as larger groups of intersecting striations (Fig. 3B). They likely represent modifications made by the bone being in contact with groups of sedimentary particles either during trampling or transportation. Clearly visible on this specimen also are the long cracks that occur along the bone's axis (Fig. 3A). They are lighter in color than the surrounding bone surface and do not contain any (darker) sediment, suggesting that they are recent in origin and resulting from drying of the bones.

3.2.3. Short and superficial composite grooves

On an avian bone fragment (F.43B) from Trench 6 (Fig. 4A–B), 2–3 mm long and 500 μm wide shallow, composite, parallel grooves are observed. Although morphologically similar to scraping marks made by an irregular cutting edge, the length of these grooves discard this interpretation since scraping marks tend to be more elongated (Fisher Jr., 1995).

3.2.4. Elongated impacts

The same specimen (F.43B from Trench 6) bears modifications consisting of numerous 200–800 μm long individual subparallel impacts (Fig. 4C).

3.2.5. Rows of micropits

Specimen F.702 (Fig. 5A–B) displays a set of parallel 1–2 mm long rows of 50–200 μm long elongated pits. On the other side of the bone, a similar arrangement of modifications is observed. This pattern may have been produced by a small vertebrate chewing the shaft. On specimen F.753 (Fig. 5C–D), the primary bone is missing over a large area of the diaphysis, the scar edge has a crenulated morphology and the surface of the exposed inner bone is covered by curved striations. In one

Table 2
Bone surface modifications that were recorded on the 20 avian specimens from Mata Menge.

Trench	Int[a]	Nr	Taxon	Element	Description of modification	Interpretation[b],[c]
32C	u	F.753	Aves	Long bone fragment	Rows of pits	**Bite marks**
32D	u	F.657	cf. *Tadorna*	Coracoid	Overlapping, polydirectional spindle-like striations and two parallel striations.	Sediment marks?
32F	u	F.156	Aves	Long bone fragment	Small overlapping spindle-like striations	Sediment marks
31	1	F.1031	Aves	Long bone fragment	Shallow individual parallel grooves.	Sediment marks?
31	1	F.1681	Aves	Long bone fragment	Composite parallel marks that remove the manganese, and etch pits.	Preparation marks, etching
31	1	F.1692	Medium bird	Long bone fragment	Small composite parallel marks	**Scraping marks?**
30	1	F.146	Aves	Long bone fragment	Individual parallel grooves	Not diagnostic enough
30	1	F.351	Aves	Long bone fragment	Small spindle-like striations	Sediment marks?
30	1	F.78	Large bird	Phalanx	Etch pits	Etching
30B	1	F.166	Anatidae sp.	Left radius	Individual parallel grooves	Preparation marks
27	1	F.1469	*Cygnus* sp.	Long bone fragment	Individual short curved marks, lighter internally	Preparation marks
27B	1	F.1297	Aves	Long bone fragment	No diagnostic surface modifications	Sediment marks of at least 2 sets of particles. Also shows the beginning of etching
27B	1	F.2802	*Cygnus* sp.	Distal radius	Overlapping spindle-like striations in different sizes, faint etch pits	Sediment marks
27B	1	F.2803	Aves	Long bone fragment	Overlapping spindle-like striations and small impacts	Sediment marks
24	1	F.101	Aves	Long bone fragment	Individual short parallel marks, lighter color internally	Preparation marks
23A	1	F.693	Aves	Long bone fragment	Deep composite parallel marks with sediment inside.	**Scraping marks?**
23A	1	F.702	Aves	Long bone fragment	Rows of pits and curved striations	**Bite marks by a small vertebrate**
23D	1	F.1463	Medium bird	Long bone fragment	Deep and short individual parallel marks, light internal color	Preparation marks
21	1	F.125	*Cygnus* sp.	Distal left tibiotarsus	No diagnostic surface modifications	
6	1	F.43B	Aves	Long bone fragment	Several sets of composite parallel grooves, as well as elongated impacts	**Scraping and percussion marks?**

[a] Interval refers to the upper or lower fossil-bearing beds.
[b] "Preparation marks" refer to any marks that appear to be of recent origin and were likely made during the excavation and preparation process.
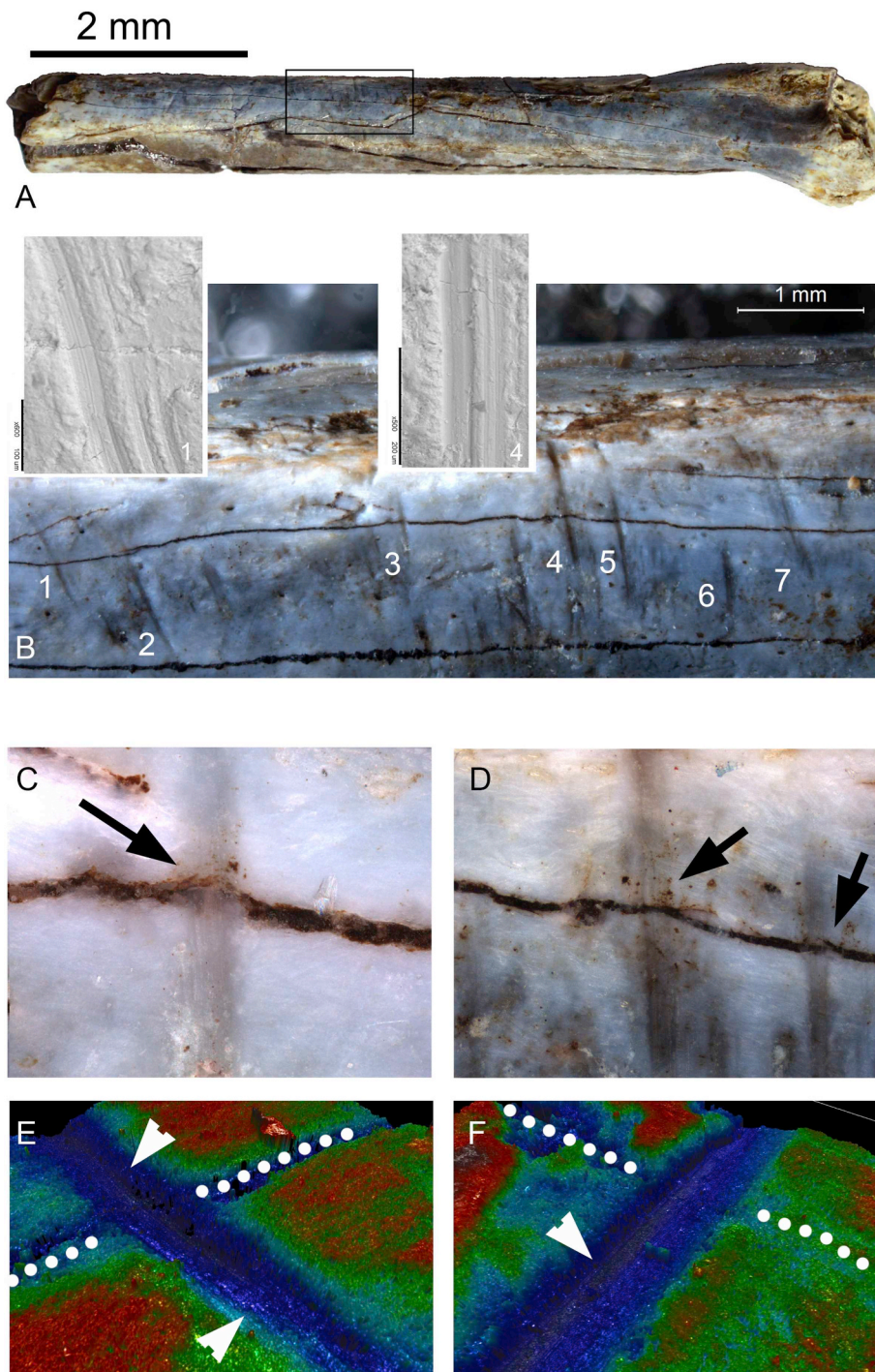[c] Bold indicates a biological agent (including hominins).

Fig. 2. Confocal microscopy and Sensofar 3D surface images of an anatid ulna (F.166, Geology Museum) from Mata Menge. A. Ventral view of the distal right ulna with box indicating location of linear marks. B. Close up of the seven major marks, including Environmental Scanning Electron Microscope images of marks 1 and 4. C. Confocal microscope image of mark 3 with arrow indicating upwards displaced sediment from crack. D. Confocal microscope image of marks 4 and 5 with arrows indicating displaced sediment from crack. E. Sensofar 3D image of the surface of mark 3, with arrows indicating the mark with its internal striations extending over the crack (dotted line). F. Sensofar 3D image of the surface of marks 4 and 5, with arrows indicating the mark with its internal striations extending over the crack (dotted line).

case the striations are clearly originating from two circular pits located at the edge of the scar. These pits are probably punctures produced by the cuspids of a small tooth. Striations stemming from the punctures likely derive from the displacement of the tooth across the bone surface after the bite. Even if less striking, a similar pattern is observed in other areas of the scar.

3.2.6. Etch pits

A number of specimens from both the upper and lower fossiliferous intervals show signs of acid etching. This can range from an initial stage where the bone shows lighter patches of surface coloring but no holes, as seen in F.2802 (Fig. 3C), to more extreme cases in which the outer bone layer is removed and subovoidal 300–800 μm long pits appear on the bone surface (Fig. 6). In specimen F.1681, a long bone fragment from Trench 31, the etch pits are bordered by a thin ring of manganese that likely was there before the etching commenced. This may indicate that the acid etching appears to have taken place on locations where the manganese was already present. Whether this reflects a preference of the acid to manganese-affected bone is unclear.
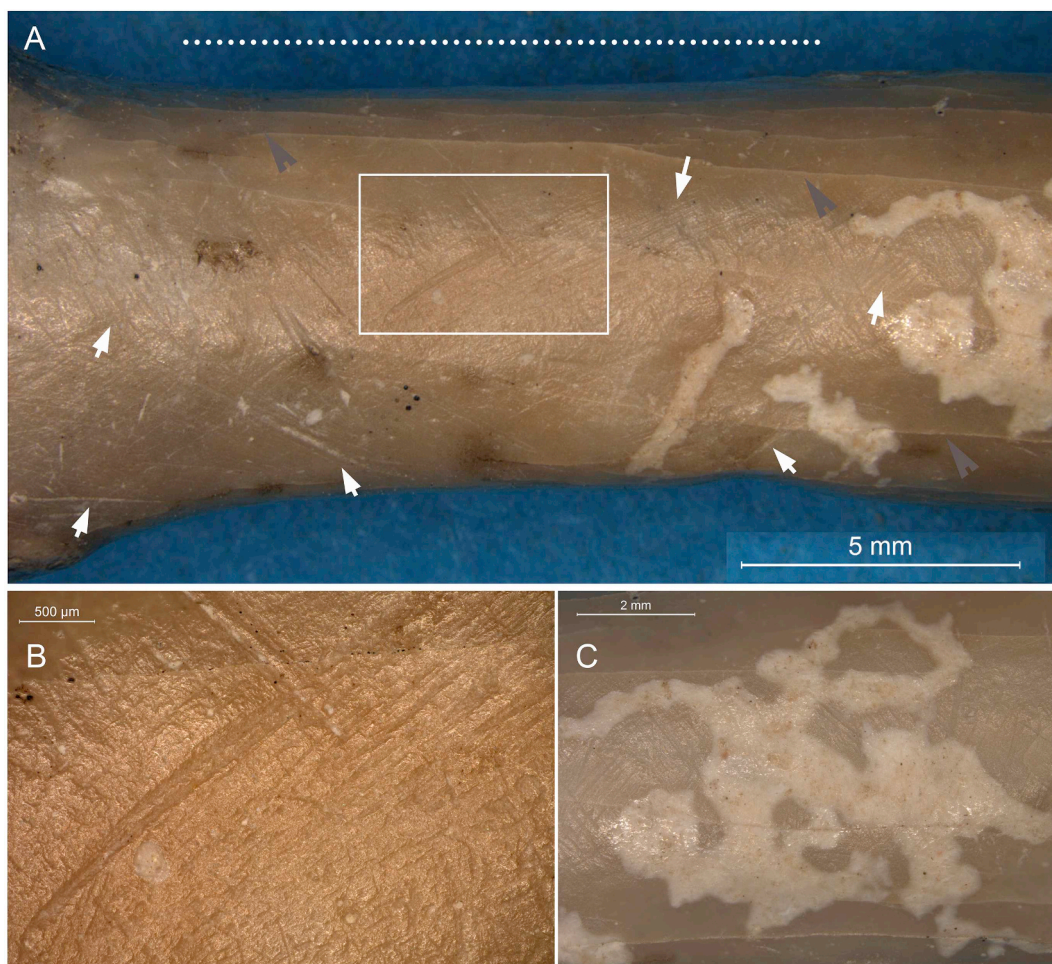
Fig. 3. A. Close up of F.2802 (Trench 27B, Geology Museum), with several sets of large and small overlapping spindle-like striations all over the bone surface. B. Close-up of a set of intersecting striations in A. C. Close up of white patches interpreted as an initial stage of acid etching. Arrows indicate overlapping spindle-like striations, grey arrowheads indicate cracks in parallel with the bone's long axis, indicated by the dotted line.

4. Discussion

Our analysis of bone surfaces in the Mata Menge avian bone assemblages has documented a number of intriguing bone surface modifications. It suggests that several taphonomic agents were at play during and after the accumulation of the Mata Menge small vertebrate assemblage. The absence of mammalian carnivores on Pleistocene Flores leaves only crocodiles, Komodo dragons, and, potentially, hominins as large-bodied taphonomic agents. The pits and scores observed on specimen F.753 are in the size range of Komodo dragons as reported by D'Amore and Blumenschine (2009), but it is unclear if Komodo dragons would leave tooth marks on small vertebrate remains. We did not observe any marks that could be attributed to crocodiles, but, similarly to Komodo dragons, these large-bodied reptiles may have swallowed prey of this size whole. Close examination of the bone surfaces of the *Stegodon* assemblage may reveal if Komodo dragons or crocodiles contributed to the So'a Basin large vertebrate assemblage. In addition, feeding experiments in which these two reptiles are fed small mammal and bird carcasses could possibly elucidate if they leave any marks on small vertebrate remains. It should be noted that the two circular pits on specimen F.753 (Fig. 5C–D) are also reminiscent of human tooth marks (Fernández-Jalvo and Andrews, 2017; Morales-Pérez et al., 2017). The two pits are located at the edge of the scar and

form a crenulated scar edge, and have a set of curved striations originating from them. These features are often associated with human chewing of bone (Romero et al., 2016; Fernández-Jalvo and Andrews, 2017; Morales-Pérez et al., 2017). However, given the complexity of identifying human tooth marks and the unknowns regarding potential Komodo dragon tooth marks, more analyses and comparative material is needed to before one can firmly attribute these marks to hominins.

The molar imprints on both sides of specimen F.702 can be attributed to a small mammal, possibly a shrew. Soricids mainly feed on insects, but they scavenge small vertebrate carcasses and leave marks comparable to those of large carnivores but smaller in size (Andrews, 1990; Fernández-Jalvo and Andrews, 2017). Although no shrews have been recovered from the So'a Basin as of yet, it should be noted that Flores hosts the endemic shrew *Suncus mertensi* Kock, 1974, as well as the more widespread *S. murinus* and *Crocidura monticola* (Musser, 1981). The recovery of shrew remains from Late Pleistocene and Holocene deposits at Liang Bua (van den Hoek Ostende et al., 2006) raise the possibility that shrews were present in the Middle Pleistocene as well.

A number of bones display polydirectional and subparallel scratches (such as seen in Fig. 3) that we interpret as marks resulting from contact with one or more sediment particles either during trampling by other animals or transportation through sediment. Distinguishing trampling
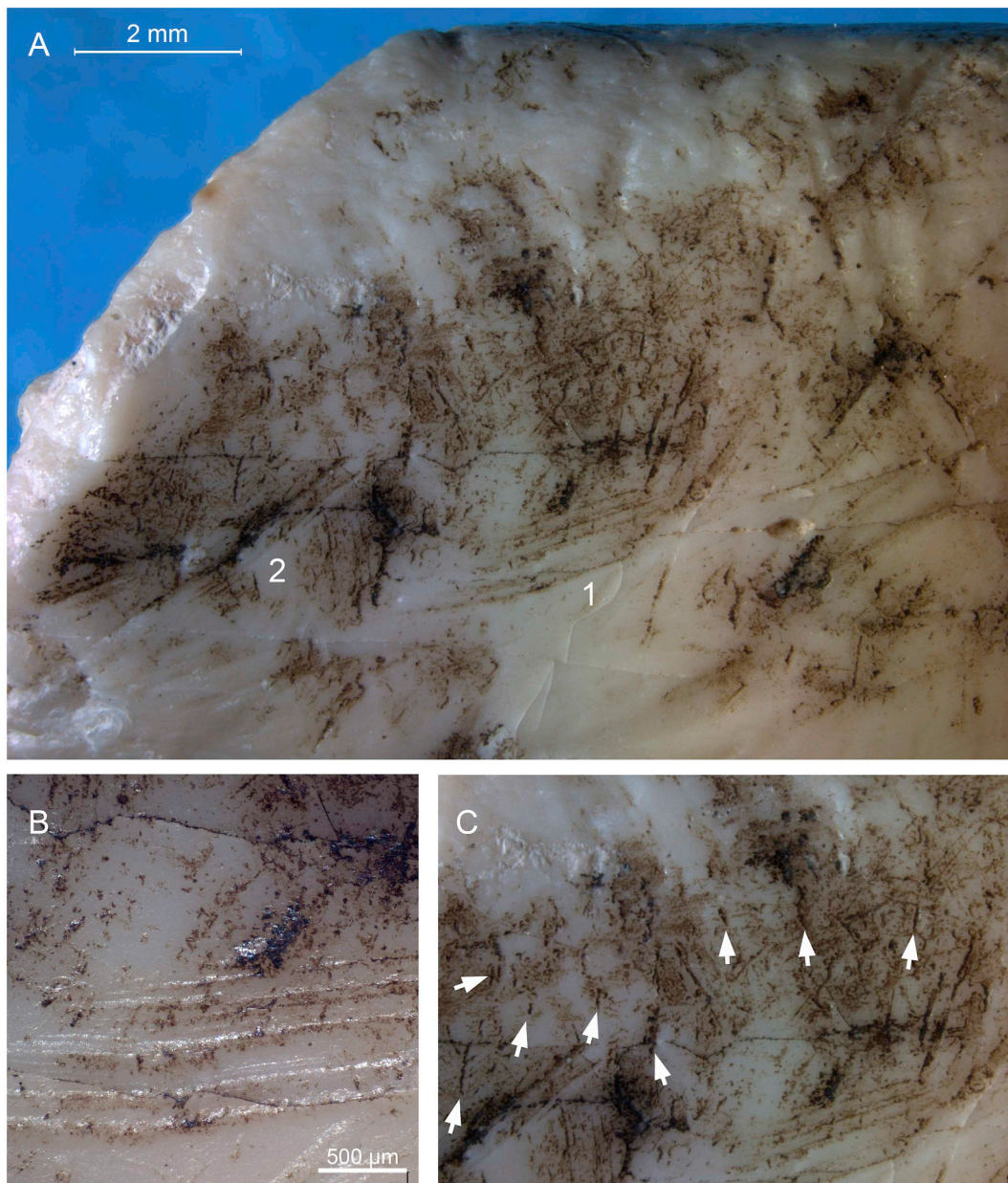
Fig. 4. Multifocus images of a bone fragment (F.43B, Geology Museum) from Trench 6. A. Area showing multiple composite wide, superficial grooves. B. Close-up of groove 1. C. Close-up of bone surface with several elongated pits (arrows).

marks from other types of sedimentary abrasion is difficult (Olsen and Shipman, 1988), as both result in fine, individual grooves that lack internal striations and a definite preferred orientation, and are distributed widely across the bone surface (Fisher Jr., 1995). Animals like *Stegodon*, and potentially hominins and Komodo dragons, walking over bones on a stony substrate might have produced some of the marks observed here. Specimens from both the upper and lower fossiliferous intervals, which both represent deposits of small, sinuous stream tributaries, display such sedimentary abrasion marks. This suggests that these marks might have resulted from natural sediment abrasion, likely during transportation by the mudflows from the Welas Caldera that transported the bones. The origin of the severe etching observed on F.1681 (and somewhat on F.2802) and why it occurs on areas stained by manganese is unclear. Acidic components from the volcanic ash may

be a factor. Alternatively, it may be the result of bacterial growth. Root etching is unlikely since modifications produced by this agent are generally dendriform and show irregular inner surfaces, which is not the case here.

Several bones display surface modifications that, at first glance, are not morphologically different from intentional marks made by stone tools, such as the parallel grooves on F.166 (Fig. 2) and the composite superficial grooves and elongated impacts on F.43B (Fig. 4). The systematic exploitation of birds was once considered a behaviour exclusive to modern humans (Klein, 1989), but has now also been observed in Neanderthals (Blasco et al., 2014; Gómez-Olivencia et al., 2018; Finlayson et al., 2016) and may even extend back into the Middle Pleistocene (Blasco and Fernández Peris, 2012). The origin of the close relationship between hominins and birds may have been symbiotic
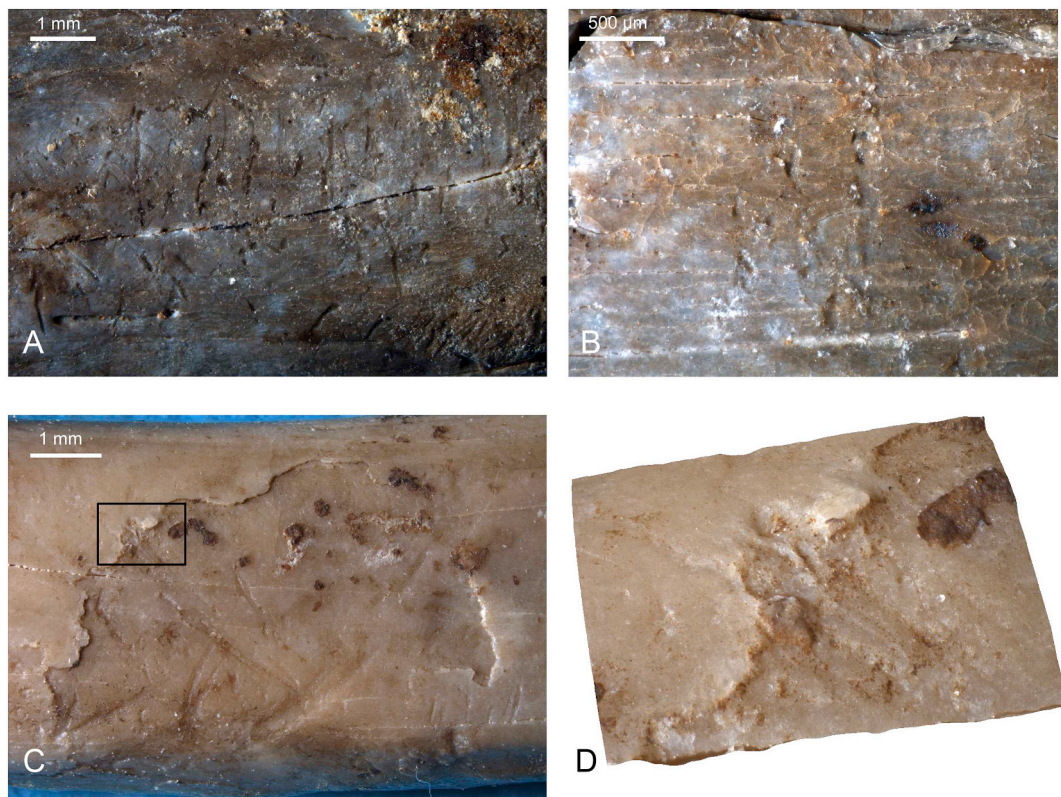
Fig. 5. Rows of micropits on bird remains from Mata Menge interpreted as bite marks. A. Rows of bites on specimen F.702 (Geology Museum). B. Close up of other side of the bone showing similar rows of marks. C. F.753 (Geology Museum) showing the flaking off of a primary bone lamella associated with curve composite striations stemming from the scar edges. D. 3D reconstruction of box in C showing two pits and grooves coming out of them interpreted as bite and scoring marks.

(Finlayson et al., 2016); early hominins may have benefitted in locating food by observing scavenging birds, while scavenging birds may have benefitted from food remains left over after a hunt. At Liang Bua, *Homo floresiensis* is closely associated with scavenging birds, but there is no evidence for the exploitation of birds as a food source. Nevertheless, it is clear that the close association between hominins and scavenging birds predates the arrival of modern humans in Wallacea. This behaviour could have arisen independently in the lineage culminating in *Homo floresiensis*. Alternatively, it may have originated in the common ancestor of *H. floresiensis*, *H. neanderthalensis* and *H. sapiens*. If the latter is indeed the case, we should expect to see evidence for close associations between hominins and scavenging birds in the Early and Middle Pleistocene sites on Flores as well.

Yet, despite the presence of hominin skeletal remains and associated stone tools, we find no unambiguous evidence for exploitation of birds by the So'a Basin hominins, or for hominins being a significant accumulating agent for avian remains at Mata Menge. The short, parallel striations on the anatid radius appeared good candidates for hominin cut marks. With optical microscopes under reflected light as well as the naked eye, the marks looked like genuine cut marks; they are of the same color as the bone itself, and sediment particles are visible in some of them. However, the internal striations continuing across the crack and the displaced sediment particles identified by confocal microscopy, argue against these marks being hominin cut marks. Rather, it suggests that the marks were made well after the cracks appeared in the bone and became filled with sediment. It is still possible that these marks were made by an anthropogenic agent, but likely much more recently

than following their initial burial and fossilization, and quite possibly during or shortly after excavating. The fact that the marks and the bone surface do not show any perceptible difference in color cannot be used to argue in favor of the antiquity of the marks as a lack of discoloration can occur when the outer bone layer and the bone beneath are similar in color. A recent origin of the marks would also explain why the internal striations are so well preserved and look so remarkably "fresh" (see Fig. 2B). Alternatively, the marks could have been formed after fossilization of the bone in the sediments, but before final burial. The sediments in both the lower and upper fossil-bearing levels at Mata Menge are thought to have been accumulated in stream valleys on a volcanic apron. During periods of low volcanic activity, the streams cut down into their own aprons, while during periods of volcanic eruptions that generated large quantities of sediment, the valleys were rapidly filled with sediment. It is conceivable that during these cycles of volcanic activity, fossilized bone was eroded out of the sediments, transported, and then deposited and buried again.

5. Conclusions

Our work presented here is the first to use multifocus and confocal microscopy to examine taphonomic bone surface modifications on small vertebrate remains from an Early to Middle Pleistocene site in Insular South East Asia. We observed a range of intriguing taphonomic modifications demonstrating the action of several taphonomic agents, and we propose a diagnosis for a number of them. However, we found no unambiguous evidence for a potential role of hominins as
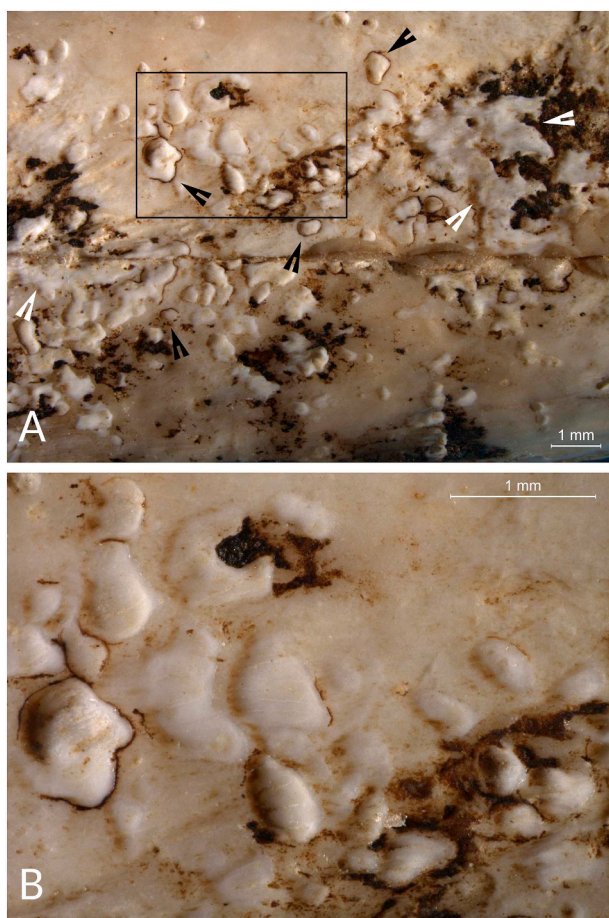
Fig. 6. A. Acid etching on Detail of F.1681 (Geology Museum). Many showing etch pits. Many pits are surrounded by a ring of manganese (black arrowheads). On both the right and left sides of the image. The larger white patches can be seen where patch on the right of A appears to have removed a large pre-existing spot of manganese (white arrowheads) appear to have been removed. B. Close-up view of box in A showing evidence of the same phenomenon.

accumulating agents in the Mata Menge avian assemblage. Given that direct comparative data are lacking, our work should be seen as preliminary. Data on the morphology and frequency of bone surface modifications by relevant biological agents, data from controlled experimental settings, as well as more precise evaluation of site formation processes would greatly increase our understanding of the taphonomy of the So'a Basin.

References

Andrews, P., 1990. Owls, Caves, and Fossils: Predation, Preservation, and Accumulation of Small Mammal Bones in Caves, With an Analysis of the Pleistocene Cave Faunas From Westbury-Sub-Mendip. University of Chicago Press, Somerset, pp. 1–231.

Aziz, F., van den Bergh, G.D., Morwood, M.J., Hobbs, D.R., Kurniawan, I., Collins, J. Jatmiko, 2009. Excavations at Tangi Talo, central Flores, Indonesia. In: Aziz, F., Morwood, M.J., van den Bergh, G.D. (Eds.), Pleistocene geology, palaeontology and archaeology of the Soa Basin, Central Flores, Indonesia. Special publication no. 36. Pusat Survei Geologi, Bandung, pp. 41–58.

Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. Paleobiol. 4, 150–162.

van den Bergh, G.D., Aziz, F., Kurniawan, I., Morwood, M.J., Lentfer, C.J., Suyone, Setiawan R., 2009. Environmental reconstruction of the Middle Pleistocene archaeological and palaeontological site of Mata Menge, Central Flores, Indonesia. In: Aziz, F., Morwood, M.J., van den Bergh, G.D. (Eds.), Pleistocene geology, palaeontology and archaeology of the Soa Basin, Central Flores, Indonesia. Special publication no. 36. Pusat Survei Geologi, Bandung, pp. 58–94.

van den Bergh, G., Brumm, A., Puspaningrum, M., Setiabudi, E., Kurniawan, I., Prasetyo, U., 2014. Taphonomy of Stegodon florensis remains from the early Middle Pleistocene archaeological site Mata Menge, Flores, Indonesia. In: Abstract Book of the VIth International Conference on Mammoths and Their Relatives. S.A.S.G., Special Volume 102, pp. 207–208.

van den Bergh, G.D., Kaifu, Y., Kurniawan, I., Kono, R.T., Brumm, A., Setiyabudi, E., Aziz, F., Morwood, M.J., 2016. *Homo floresiensis*-like fossils from the early Middle Pleistocene of Flores. Nature 534, 245–248.

Blasco, R., Fernández Peris, J., 2012. A uniquely broad spectrum diet during the Middle Pleistocene at Bolomor Cave (Valencia, Spain). Quat. Int. 252, 16–31.

Blasco, R., Finlayson, C., Rosell, J., Sánchez Marco, A., Finlayson, S., Finlayson, G., José Negro, J., Giles Pacheco, F., Rodriguez Vidal, J., 2014. The earliest pigeon fanciers. Sci. Rep. 4, 5971.

Blumenschine, R.J., 1989. A landscape taphonomic model of the scale of prehistoric scavenging opportunities. J. Hum. Evol. 18 (4), 345–371.

Bouteaux, A., Moigne, A.-M., 2010. New taphonomical approaches: the Javanese Pleistocene open-air sites (Sangiran, central Java). Quat. Int. 223–224, 220–225.

Bouteaux, A., Moigne, A.-M., Sémah, F., Jacob, T., 2007. Les assemblages fauniques associés aux sites à *Homo erectus* du dôme de Sangiran (Pléistocène moyen, Java, Indonésie). C. R. Palevol 6 (3), 169–179.

Brain, C.K., 1981. The Hunters or the Hunted? An Introduction to African Cave Taphonomy. Univ of Chicago Press, Chicago.

Brumm, A., Aziz, F., van den Bergh, G.D., Morwood, M.J., Moore, M.W., Kurniawan, I., Hobbs, D.R., Fullagar, R., 2006. Early stone technology on Flores and its implications for *Homo floresiensis*. Nature 441, 624–628.

Brumm, A., Moore, M.W., Kurniawan, I., Suyono, R.S., Jatmiko, Morwood, M.J., Aziz, F., 2009. Early Pleistocene stone technology at Mata Menge, central Flores, Indonesia. In: Aziz, F., Morwood, M.J., van den Bergh, G.D. (Eds.), Pleistocene Geology, Paleontology and Archaeology of the Soa Basin, Central Flores, Indonesia. Special Publication No. 36. Pusat Servei Geologi, Bandung, pp. 119–137.

Brumm, A., van den Bergh, G.D., Storey, M., Kurniawan, I., Alloway, B.V., Setiawan, R., Setiyabudi, E., Grün, R., Moore, M.W., Yurnaldi, D., Puspaningrum, M.R., Wibowo, U.P., Insani, H., Sutisna, I., Westgate, J.A., Pearce, N.J.G., Duval, M., Meijer, H.J.M., Aziz, F., Sutikna, T., van der Kaars, S., Flude, S., Morwood, M.J., 2016. Age and context of the oldest known hominin fossils from Flores. Nature 534, 249–253.

Choi, K., Driwantoro, D., 2007. Shell tool use by early members of *Homo erectus* in Sangiran, central Java, Indonesia: cut mark evidence. J. Archaeol. Sci. 34, 48–58.

Courtenay, L.A., Yravedra, J., Maté-González, M.Á., Aramendi, J., González-Aguilera, D., 2017. 3D analysis of cut marks using a new geometric morphometric methodological approach. Archaeol. Anthropol. Sci. 1–15.

Courtenay, L.A., Maté-González, M.Á., Aramendi, J., Yravedra, J., González-Aguilera, D., Domínguez-Rodrigo, M., 2018. Testing accuracy in 2D and 3D geometric morphometric methods for cut mark identification and classification. PeerJ 6, e5133.

D'Amore, D.C., Blumenschine, R.J., 2009. Komodo monitor (*Varanus komodoensis*) feeding behavior and dental function reflected through tooth marks on bone surfaces, and the application to ziphodont paleobiology. Paleobiol. 35 (4), 525–552.

Domínguez-Rodrigo, M., Barba, R., Egeland, C.P., 2007. Deconstructing Olduvai: A Taphonomic Study of the Bed I Sites. Springer, Dordrecht, pp. 1–292.

Fernández-Jalvo, Y., Andrews, P., 2017. Atlas of Taphonomic Identifications. Vertebrate Paleobiology and Paleoanthropology Series. Springer, Dordrecht, pp. 1–359.

Finlayson, C., Finlayson, S., Guzman, F.G., Sánchez Marco, A., Finlayson, G., Jennings, R., Giles Pacheco, F., Rodriguez Vidal, J., 2016. Using birds as indicators of Neanderthal environmental quality: Gibraltar and Zafarraya compared. Quat. Int. 421, 32–45.

Fisher Jr., J.W., 1995. Bone surface modifications in zooarchaeology. J. Archaeol. Method. Th. 2 (1), 7–68.

Gómez-Olivencia, A., Sala, N., Núñez-Lahuerta, C., Sanchis, A., Arlegi, M., Rios-Garaizar, J., 2018. First data of Neandertal bird and carnivore exploitation in the Cantabrian

Region (Axlor; Barandiaran excavations; Dima, Biscay, Northern Iberian Peninsula). Sci. Rep. 8, 10551.

Gümrükçü, M., Pante, M.C., 2018. Assessing the effects of fluvial abrasion on bone surface modifications using high-resolution 3-D scanning. J. Arch. Sci. Rep. 21, 208–221.

Harris, J.A., Marean, C.W., Ogle, K., Thompson, J., 2017. The trajectory of bone surface modification studies in paleoanthropology and a new Bayesian solution to the identification controversy. J. Hum. Evol. 110, 69–81.

Hawkins, S., O'Connor, S., Louys, J., 2017. Taphonomy of bird (Aves) remains at Laili Cave, Timor-Leste, and implications for human-bird interactions during the Pleistocene. Archaeol. Anthrop. Sci. 1–13.

Hawkins, S., Samper Carro, S., Louys, J., Aplin, K., O'Connor, S., Mahirta, 2018. Human palaeoecological interactions and owl roosting at Tron Bon Lei, Alor Island, eastern Indonesia. J. Island Coast. Archaeol. 13 (3), 371–387.

van den Hoek Ostende, L.W., van den Bergh, G.D., Awe Due, R., 2006. First fossil insectivores from Flores. Hell. J. Geosc. 41, 67–72.

Ingicco, T., van den Bergh, G.D., Jago-on, C., Bahain, J.-J., Chacón, M.G., Amano, N., Forestier, H., King, C., Manalo, K., Nomade, S., Pereira, A., Reyes, M.C., Sémah, A.-M., Shao, Q., Voinchet, P., Falguères, C., Albers, P.C.H., Lising, M., Lyras, G., Yurnaldi, D., Rochette, P., Bautista, A., de Vos, J., 2018. Earliest known hominin activity in the Philippines by 709 thousand years ago. Nature 557, 233–237.

Joordens, J.C.A., d'Errico, F., Wesselingh, F.P., Munro, S., de Vos, J., Wallinga, J., Ankjærgaard, C., Reimann, T., Wijbrans, J.R., Kuiper, K.F., Mücher, H.J., Coqueugniot, H., Prié, V., Joosten, I., van Os, B., Schulp, A.S., Panuel, M., van der Haas, V., Lustenhouwer, W., Reijmer, J.J.G., Roebroeks, W., 2015. *Homo erectus* at Trinil on Java used shells for tool production and engraving. Nature 518, 228–231.

Klein, R.G., 1989. The Human Career. University of Chicago Press, Chicago, pp. 1–524.

Kock, D., 1974. Eine neue *Suncus*-Art von Flores. Kleine Sunda-Inseln. Sencken. Biol. 55, 197–203.

Louys, J., Kealy, S., O'Connor, S., Price, G., Hawkins, S., Aplin, K., Rizal, Y., Zaim, J., Mahirta, Tanudirjo, D.A., Santoso, W.D., Hidayah, A.R., Trihascaryo, A., Wood, R., Bevitt, J., Clark, T., 2017. Differential preservation of vertebrates in Southeast Asian caves. Int. J. Spel. 46, 379–408.

Maringer, J., Verhoeven, T., 1970. Die Steinartefakte aus der Stegodon-Fossilschicht von Mengeruda auf Flores. Indonesien. Anthropos 65 (1/2), 229–247.

Meijer, H.J.M., Sutikna, T., Saptomo, W.E., Due, R.A., Wasisto, S., James, H.F., Morwood, M.J., Tocheri, M.W., 2013. Late Pleistocene-Holocene non-Passerine Avifauna of Liang Bua (Flores, Indonesia). J. Vertebr. Paleontol. 33 (4), 877–894.

Meijer, H.J.M., Kurniawan, I., Setiabudi, E., Brumm, A., Sutikna, T., Setiawan, R., van den Bergh, G.D., 2015. Avian remains from the Early/Middle Pleistocene of the So'a Basin, central Flores, Indonesia, and their palaeoenvironmental significance. Palaeogeogr. Palaeocl. Palaeoecol. 440, 161–171.

Moore, M.W., Sutikna, T., Jatmiko, Morwood, M.J., Brumm, A., 2009. Continuities in stone flaking technology at Liang Bua, Flores, Indonesia. J. Hum. Evol. 57, 503–526.

Morales-Pérez, J.V., Salazar-García, D.C., de Miguel Ibáñez, M.P., Miret, i Estruch, C., Jordá Pardo, J.F., Verdasco Cebrián, C.C., Pérez Ripoll, M., Aura Tortosa, J.E., 2017. Funerary practices or food delicatessen? Human remains with anthropic marks from the Western Mediterranean Mesolithic. J. Anthropol. Archaeol. 45, 115–130.

Morley, M.W., Goldberg, P., Sutikna, T., Tocheri, M.W., Prinsloo, L.C., Jatmiko, Saptomo, E.W., Wasisto, S., Roberts, R.G., 2017. Initial micromorphological results from Liang Bua, Flores (Indonesia): Site formation processes and hominin activities at the type locality of *Homo floresiensis*. J. Arch.Sci. 77, 125–142.

Morwood, M.J., O'Sullivan, P., Aziz, F., Raza, A., 1998. Fission track age of stone tools and fossils on the east Indonesian island of Flores. Nature 392, 173–176.

Musser, G.G., 1981. The giant rat of Flores and its relatives east of Borneo and Bali. Bull. Am. Mus. Nat. Hist. 169 (2), 67–176.

Njau, J., Blumenschine, R., 2006. A diagnosis of crocodile feeding traces on larger mammal bone, with fossil examples from the Plio-Pleistocene Olduvai Basin, Tanzania. J. Hum. Evol. 50, 142–162.

Olsen, S.L., Shipman, P., 1988. Surface modification on bone: trampling versus butchery. J. Archaeol. Sci. 15 (5), 535–553.

O'Sullivan, P.B., Morwood, M.J., Hobbs, D., Aziz, F., Suminto, M.S., Raza, A., Maas, R., 2001. Archaeological implications of the geology and chronology of the Soa Basin, Flores, Indonesia. Geology 29 (7), 607–610.

Otárola-Castillo, E., Torquato, M., Hawkins, H.C., James, E., Harris, J., Marean, C., McPhernon, S., Thompson, J., 2018. Differentiating between cutting actions on bone using 3D geometric morphometrics and Bayesian analyses with implications to human evolution. J. Arch. Sci. 89, 56–67.

Pante, M.C., Muttart, M.V., Keevil, T.L., Blumenschine, R.J., Njau, J.K., Merritt, S.R., 2017. A new high-resolution 3-D quantitative method for identifying bone surface modifications with implications for the Early Stone Age archaeological record. J. Hum. Evol. 102, 1–11.

Pickering, T.R., Schick, K., Toth, N. (Eds.), 2007. Breathing Life into Fossils: Taphonomic Studies in Honor of C.K. (Bob) Brain. Stone Age Institute Publication Series 2. Stone Age Institute, pp. 1–307.

Romero, A.J., Díez, J.C., Rodríguez, L., Arceredillo, D., 2016. Anthropic fractures and human tooth marks: An experimental approach to non-technological human action on avian long bones. Quat. Intern. 421, 219–227.

Sahle, Y., El Zaatari, S., White, T.D., 2017. Hominid butchers and biting crocodiles in the African Plio–Pleistocene. Proc. Nat. Ac. Sci. 114 (50), 13164–13169.

Suminto, Morwood, M.J., Kurniawan, I., Aziz, F., van den Bergh, G.D., Hobbs, D.R., 2009. In: Aziz, F., Morwood, M.J., van den Bergh, G.D. (Eds.), *Pleistocene geology, palaeontology and archaeology of the Soa Basin, Central Flores, Indonesia*. Special publication no. 36. Pusat Survei Geologi, Bandung, pp. 19–40.

Sutikna, T., Tocheri, M.W., Faith, T., Jatmiko, Due, Awe, R., Meijer, H.J.M., Saptomo, E.W., Roberts, R.G., 2018. The spatio-temporal distribution of archaeological and faunal finds at Liang Bua (Flores, Indonesia) in light of the revised chronology for *Homo floresiensis*. J. Hum. Evol. 124, 52–74.

Veatch, E.G., Tocheri, M.W., Sutikna, T., McGrath, K., Saptomo, E.W., Jatmiko, Helgen, 2019. Temporal shifts in the distribution of murine rodent body size classes at Liang Bua (Flores, Indonesia) reveal new insights into the paleoecology of *Homo floresiensis* and associated fauna. J. Hum. Evol. 130, 45–60.

Vietti, L.A., 2016. Quantifying bone weathering stages using the average roughness parameter Ra measured from 3D data. Surf Topogr. 4, 034006.

West, J.A., Louys, J., 2007. Differentiating bamboo from stone tool cut marks in the zooarchaeological record, with a discussion on the use of bamboo knives. J. Arch. Sci. 34, 512–518.

Yravedra, J., Maté-González, M.A., Palomeque, J.F., Aramendi, J., Estaca-Gómez, V., San-Juan-Blázquez, M., García-Vargas, E., Organista, E., González-Aguilera, D., Arriaza, M.A., Cobo-Sçanchez, L., Gidna, A., Uribelarrea, D., Baquedano, E., Mabulla, A., Domínguez-Rodrigo, M., 2017. A new approach to raw material use in the exploitation of animal carcasses at BK (Upper Bed II, Olduvai Gorge, Tanzania): a micro-photogrammetric and geometric morphometric analysis of cut marks. Boreas 46 (4), 860–873.

Yravedra, J., Aramendi, J., Maté-González, M.Á., Austin Courtenay, L., González-Aguilera, D., 2018. Differentiating percussion pits and carnivore tooth pits using 3D reconstructions and geometric morphometrics. PLoS One 13 (3), e0194324.