Journal of Human Evolution xxx (2017) 1–16

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

The paleoecology of Pleistocene birds from Middle Bed II, at Olduvai Gorge, Tanzania, and the environmental context of the Oldowan-Acheulean transition

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ARTICLE INFO

Article history:
Received 23 December 2016
Accepted 14 November 2017
Available online xxx

Keywords:
Taphonomy
Paleoenvironment
African ornithology
Homo habilis
Homo erectus/ergaster

ABSTRACT

Fossil bird data (community composition and taphonomic profiles) are used here to infer the environmental context of the Oldowan-Acheulean transitional period at Olduvai Gorge, Tanzania. This is the first comprehensive report on the Middle Bed II avifauna and includes fossils excavated by the Olduvai Geochronology and Archaeology Project (OGAP) and recently rediscovered fossils collected by Mary Leakey. Crane, ibis, darter, owl, raptor, crow, and vulture are reported from Bed II for the first time. The presence of these taxa, absent earlier in this Bed, point to a general opening and drying of the landscape with grassland and open woodland expansion. Taxa associated with dense, emergent wetland vegetation, such as dabbling ducks and rails, are uncommon and less diverse than earlier in Bed II. This suggests more mature wetlands with clearer waters. Cormorants continue to be common, but are less diverse. Cormorants and other roosting taxa provide evidence of trees in the area. Compared to lowermost Bed II, the Middle to Upper Bed II landscape is interpreted here as more open and drier (but not necessarily more arid), with matured wetlands, scattered trees, and a greater expansion of grasslands.

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1. Introduction

The Pleistocene birds of Olduvai Gorge, Tanzania, remain the largest and richest avifaunal assemblage known in Africa (Wetmore, pers. comm., in Leakey, 1965; Brodkorb, 1985) and provide important data on avian evolution and community change on that continent (e.g., Harrison, 1980a; Brodkorb, 1985; Prassack, 2010, 2014). The Olduvai birds are also important to the field of paleoanthropology, as they come from a dynamic period of hominin evolution at a site internationally recognized for its paleoanthropological significance (Leakey et al., 1964; Leakey, 1965, 1971; Tobias, 1967, 1991; Blumenschine et al., 2003; Clarke, 2012; Domínguez-Rodrigo et al., 2013). In this article, avifaunal data from the uppermost Lower, Middle, and lowermost Upper Bed II are used to reconstruct environmental conditions at Olduvai during the Oldowan-Acheulean stone tool transition. These birds come from excavations made by the Olduvai Geochronology and Archaeology Project (OGAP; de la Torre et al., 2012), which currently investigates the behavioral and/or environmental causalities behind the important and highly visible shift in the archaeological record from an archaic, core-and-flake Oldowan stone tool industry to the large handaxes that characterize the Acheulean.

Traditionally, the Oldowan has been associated with *Homo habilis,* while the emergence of the Acheulean is linked to *Homo erectus/ergaster* (e.g., Leakey, 1975). However, the behavioral ecologies and taxonomic affinities of the hominins involved in this transition, at Olduvai and elsewhere, and the role, if any, played by a changing environment remain unclear (Beyene et al., 2013; de la Torre and Mora, 2014; Diez Martin et al., 2015). For example, the appearance of *Homo erectus/ergaster,* sometime between 1.65 and 1.7 Ma (McDougall et al., 2012), coincides with the emergence of the Acheulean, but this technology also temporally overlaps in part with *Homo habilis* (Spoor et al., 2007) and *Paranthropus boisei* (Domínguez-Rodrigo et al., 2013). The purpose here is to provide an ecological framework from which to address the causalities behind this technological transition.

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https://doi.org/10.1016/j.jhevol.2017.11.003
0047-2484/Published by Elsevier Ltd.

1.1. Geology and early stone age archaeology at Olduvai Gorge

Olduvai Gorge is located on the eastern Serengeti Plains of northern Tanzania. The Gorge is part of the eastern branch of the East African Rift, an intra-continental ridge system that extends from Ethiopia through Kenya and into northern Tanzania. Fossil and artifact-rich exposures extend 20 km along an east-west trending Main Gorge and southerly directed Side Gorge, which meet at a fossiliferous "junction" (Leakey, 1971; Hay, 1976). Olduvai's deposits date from approximately 1.98 Ma to 15,000 BP (Hay, 1976; McHenry et al., 2007).

Early excavations at Olduvai focused on dense archaeological and fossiliferous deposits termed hominin "living floors" (e.g., Leakey, 1971). A methodological shift occurred in 1989, when the Olduvai Landscape Archaeology and Paleoanthropology Project (OLAPP) initiated a landscape mode of excavation to address environmental, community, and behavioral changes across temporally refined but spatially expansive paleolandscapes (Peters and Blumenschine, 1995; Blumenschine and Peters, 1998; Blumenschine et al., 2003, 2012a). OLAPP excavations sampled areas across the landscape, regardless of fossil or artifact densities, with a focus on understanding *Homo habilis* behavior and its use of Oldowan technologies during Bed I and lowermost Bed II times. Olduvai at that time was lacustrine-dominated, and localities occur primarily along what would have been the eastern lacustrine plain of saline-alkaline Paleolake Olduvai (Hay, 1976). Cyclical lake fluctuations (Stanistreet, 2012) coupled with frequent volcanic activity (McHenry et al., 2008; Stollhofen et al., 2008; Stollhofen and Stanistreet, 2012) facilitated burial and preservation of artifacts and faunal remains. Until the last few years, Middle Bed I and lowermost Bed II have been the focus of most archaeological research at Olduvai (e.g., Bunn and Kroll, 1986; Binford et al., 1988; Potts, 1988; Blumenschine et al., 2003, 2012b, c; Domínguez-Rodrigo et al., 2010; Pante et al., 2012; Reti, 2016).

1.2. Middle/Upper Bed II

Well-refined dates are available for Bed I and lowermost Bed II (Deino, 2012; McHenry, 2012), but Middle and Upper Bed II have a complex stratigraphy punctuated by four reworked, laterally discontinuous, and poorly dated tuffs (Tuff IIA–D: Hay, 1976; Stanistreet, 2012; McHenry et al., 2016; McHenry, 2018; Stanistreet et al., 2018). This has limited tephrostratigraphic and lithological facies control and the ability to reconstruct fossil landscapes and their representative faunal communities. Tuff IIA is variably dated from 1.66 + 0.01 Ma (Manega, 1993) to 1.72 Ma (Curtis and Hay, 1972), and McHenry (2018) has updated these dates (incorporating a more recently accepted decay constant for ^{40}K) to 1.677 Ma and 1.756 Ma, respectively. Tuff IIA was originally considered the boundary between Lower and Middle Bed II (Leakey, 1971), but Stanistreet et al. (2018; see also McHenry et al., 2016; McHenry, 2018) reassign this boundary higher up at a widespread disconformity between the Lemuta Member and overlying Lower Augitic Sandstone (Fig. 1), providing a lithostratigraphic boundary for these two sub-beds. The Bird Print Tuff (BPT in Fig. 1) has a unique geochemical fingerprint (McHenry et al., 2016) and remains useful as a local marker bed despite exhibiting some compositional heterogeneity (McHenry, 2018). Diez-Martin et al. (2015) produced a date of 1.664 Ma for a tuff, which Uribelarrea et al. (2017) place 25 cm below the actual BPT. Tuff IIB is not a true tuff and has yet to provide a reliable date (McHenry et al., 2016). Leakey (1971) placed the Middle-Upper Bed II boundary at Tuff IIC, but Tuff IIC is less widespread (McHenry, 2018) than previously thought (Hay, 1976). There is no clear lithostratigraphic boundary for separating Middle and Upper Bed II, but OGAP

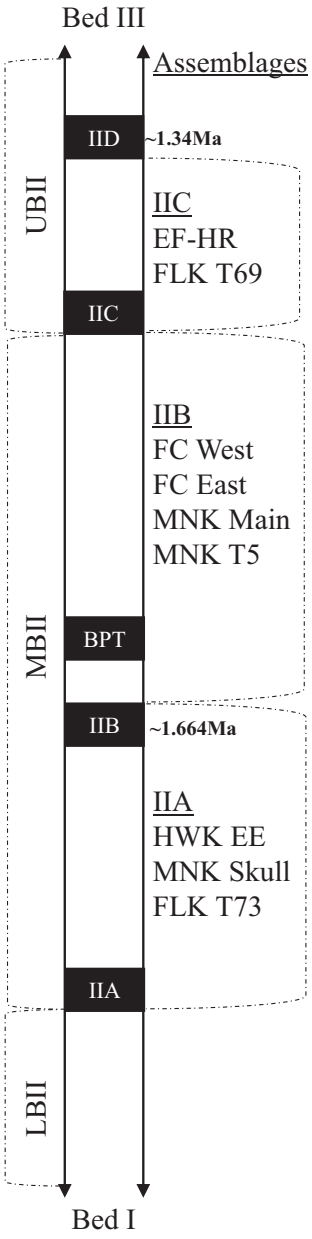

Figure 1. Schematic diagram (not to scale) of Bed II, Olduvai Gorge. Birds from each assemblage are discussed in the text. Stratigraphic placements come from Stanistreet et al. (2018) and McHenry (2018). Assemblage localities are not listed stratigraphically. Tuffs are noted as IID, IIC, BPT, IIB, and IIA. The Tuff IID date comes from Domínguez-Rodrigo et al. (2013). BPT stands for the Bird Print Tuff. A date of 1.664 Ma for the BPT (Diez-Martin et al., 2016) has been contested (Uribelarrea et al., 2017); it is likely younger.

(Stanistreet et al., 2018) maintains Leakey's (1971) Tuff IIC boundary for lack of a better marker. A Tuff IID date of 1.3386 ± 0.024 Ma (Domínguez-Rodrigo et al., 2013) is used here. The Bed II/III transition dates to at least 1.15 Ma (Hay, 1976; McHenry et al., 2007) and marks a change from a lake to a river-dominated system and a community shift reflecting greater aridity (Hay, 1976; Gentry and Gentry, 1978; Brodkorb, 1985).

1.3. Building on past avifaunal studies

Avifaunal data can provide a snapshot of local environmental and ecosystem composition and health (Pearson, 1994; Hawkins

Please cite this article in press as: Prassack, K.A., et al., The paleoecology of Pleistocene birds from Middle Bed II, at Olduvai Gorge, Tanzania, and the environmental context of the Oldowan-Acheulean transition, Journal of Human Evolution (2017), https://doi.org/10.1016/j.jhevol.2017.11.003