Sedimentological and paleoenvironmental study from Waregi Hill in the Hiwegi Formation
(early Miocene) on Rusinga Island, Lake Victoria, Kenya

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22 **Abstract**

23 Paleontological deposits on Rusinga Island, Lake Victoria, Kenya, provide a rich record of
24 floral and faunal evolution in the early Neogene of East Africa. Yet, despite a wealth of available
25 fossil material, previous paleoenvironmental reconstructions from Rusinga have resulted in
26 widely divergent results, ranging from closed forest to open woodland environments. Here, we
27 present a detailed study of the sedimentology and fauna of the early Miocene Hiwegi
28 Formation at Waregi Hill on Rusinga Island, Kenya. Our new sedimentological analyses
29 demonstrate that the Hiwegi Formation records an environmental transition from the bottom
30 to the top of the unit. Lower in the Hiwegi Formation, satin-spar calcite after gypsum in siltstone
31 deposits are interpreted as evidence for open hypersaline lakes. Moving up-section, carbonate
32 deposits – interpreted previously as evidence of aridity – are actually diagenetic calcite
33 cements, which preserve root systems of trees; further up-section, the upper-most paleosol
34 layer contains abundant root traces and tree-stump casts, previously interpreted as evidence of
35 a closed-canopy forest. These environmental differences are reflected by differences in faunal
36 composition and abundance data from Hiwegi Formation fossils sites R1 and R3. Taken
37 together, this work suggests that divergent paleoenvironmental reconstructions in previous
38 studies likely suffered from time-averaging across multiple environments. Further, our results
39 demonstrate that during the early Miocene habitats in Rusinga's Hiwegi Formation varied both
40 spatially and temporally. From a regional perspective, it has been argued that during the early
41 Neogene a broad forested environment stretched across the African continent, transitioning
42 later to predominately open landscapes that characterizes the region today. Our results
43 challenge this simple model, suggesting instead that local or regional habitat heterogeneity

44 already existed in the early Miocene. This has important implications for interpretations of the
45 selective pressures faced by early Miocene fauna, including Rusinga Island's well-preserved ape
46 and catarrhine primates.

1. Introduction

The Paleogene-Neogene transition was a time when Africa underwent tectonic, climatic, and biological changes that would eventually set up the modern ecosystems seen across East Africa today (e.g., White, 1983; Burke & Gunnell, 2008; Feakins & DeMenocal, 2010; Jacobs *et al.*, 2010; Partridge, 2010; Wichura *et al.*, 2015). During the time of the Oligocene-Miocene boundary, the Afro-Arabian plate began to collide with the Eurasian plate creating the Alpine Orogeny and simultaneously closing the western Tethys Sea which created new land connections between Africa and Eurasia (e.g., Dercourt *et al.*, 2000; Stampfli *et al.*, 2002; Golonka, 2004). Firmly stabilized by the Burdigalian (early Miocene), the connections between Africa and Eurasia established migration routes that enabled numerous faunal dispersals into and out of Africa (for instance Rögl, 1997, 1999; Sen, 2013). As a consequence, African faunas experienced major reorganization: some previously diverse clades went extinct (e.g., numerous hyrax genera, ptolemaids) whereas other groups (e.g., Proboscidea) dispersed and thrived out of Afro-Arabia (Kappelman *et al.*, 2003).

It has been argued that there was a pan-African tropical lowland forest during the early Miocene that covered Africa from west to east with little variation in broad-scale ecosystems until the eventual split of East African and Guineo-Congolian rainforests beginning at 16.8 Ma (e.g., Andrews and Van Couvering, 1975; Couvreur *et al.*, 2008; Wichura *et al.*, 2015). In contrast, it has also been argued that this idea is too simplistic, and that vegetation across Africa would have been more heterogeneous throughout the Cenozoic (e.g., Jacobs *et al.*, 1999, 2010; Jacobs, 2004). There is evidence for significant environmental heterogeneity between sites and through time, although the number of sites from the Paleogene-Neogene transition in

Africa is small (see discussion in Kappelman *et al.*, 2003). For example, there are forests during the Oligocene and Miocene in Ethiopia (Pan & Jacobs, 2009; Pan *et al.*, 2012) and Kenya (Chesters, 1957; Michel *et al.*, 2014; Oginga, 2017), but also well-documented open environments and wooded grasslands (i.e., Hamilton, 1968; Jacobs *et al.*, 1999; Kappelman *et al.*, 2003; Lukens *et al.*, 2017; Liutkus-Pierce *et al.*, 2019). While these sites offer the ability to reconstruct the environment in high-resolution, they often suffer from being temporally limited. Alternatively, more continuous records such as those from marine sediment cores or from compiled isotope values of pedogenic carbonate have contributed to the broad-scale argument that tectonic and climate shifts through the Cenozoic resulted in a major transition from more closed environments in the early Miocene to more open habitats leading up to, and particularly after, the Mid-Miocene Climatic Optimum (e.g., Ségalen *et al.*, 2007; Wichura *et al.*, 2015; Uno *et al.*, 2016; Polissar *et al.*, 2019). Ultimately, the link between small-scale environmental evidence and bigger picture ecological change is not well established. This results in part because most paleontological sites sample individual habitats that record restricted intervals of time – making it difficult to assess how quickly environmental changes may have occurred or whether multiple ecosystems existed at any one site through time.

Dated to the Burdigalian stage, Rusinga has played an important role in understanding early Neogene African paleoenvironments (e.g., Andrews & Van Couvering, 1975; Andrews *et al.*, 1979; Evans *et al.*, 1981; Collinson *et al.*, 2009) owing to its tremendous preservation of plant and animal remains. More than 100 vertebrate species are now known from the Rusinga fossil beds, as are a wide variety of remains from other fossil animals and plants (MacInnes, 1943; LeGros Clark & Leakey, 1950; Shackleton, 1951; Pickford, 1984; Walker *et al.*, 1993;

Walker, 2007; Michel *et al.*, 2014) dating between about 20-17 Ma (Peppe *et al.*, 2011, 2017b). The majority of previous research has focused on the highly fossiliferous Hiwegi Formation, and in particular strata identified as the Fossil Bed Member, from which an estimated 80% of the Rusinga fossil specimens are thought to have been derived (e.g., Van Couvering, 1972; Pickford, 1984). However, our recent work (see Michel *et al.*, 2014; Peppe *et al.*, 2017b) has shown that the “Fossil Bed Member” is not contemporaneous from site to site, as originally postulated (e.g., Andrews & Van Couvering, 1975; Andrews *et al.*, 1979; Evans *et al.*, 1981; Drake *et al.*, 1988; Collinson *et al.*, 2009). Further, we have also demonstrated that the majority of the Hiwegi Formation strata are fossiliferous (e.g., Maxbauer *et al.*, 2013; Michel *et al.*, 2014, 2017, Peppe *et al.*, 2016). This would have been a confounding factor in previous paleoenvironmental reconstructions (e.g., Evans *et al.*, 1981; Pickford, 1984) of the entire Hiwegi Formation that relied on pooled geological samples or mixed fossil assemblages based on the assumption that the “Fossil Bed Member” represented a discrete time interval across Rusinga. For this reason, it is important to revisit previous ideas about Rusinga’s environment in the early Miocene, using detailed geologic constraints for the stratigraphic position and inferred age of the fossiliferous intervals within the Hiwegi Formation (Michel *et al.*, 2014, 2017; Peppe *et al.*, 2017a; b).

Here we present new sedimentological data combined with paleosol morphology and micromorphology to reconstruct the paleoenvironments represented by the Hiwegi Formation (early Miocene) exposed on Waregi Hill, Rusinga Island. Our composite stratigraphic section through the Hiwegi Formation indicates a diversity of habitats during the early Miocene ranging from more open environments in which evaporation exceeded precipitation, to more closed-forested environments. Assessments of faunal differences between two fossil-bearing units on

Waregi Hill (R1 and R3) indicate shifts in the faunal assemblages that correspond with these paleoenvironmental changes. We propose that the early Miocene probably represented a time of climatic fluctuations in tropical East Africa, and that the tectonic shifts of the Paleogene did not result in a uniform transition from closed-canopy forests to more open habitats leading up to, and after, the Mid-Miocene Climatic Optimum (*contra* Wichura *et al.*, 2015 and references therein). Instead, there was likely a diversity of environments that existed on the continent during the early Miocene, with local factors greatly influencing individual habitats within a long-term trend of aridification.

2. Background

Rusinga Island is located in western Kenya at the eastern edge of Lake Victoria, along the flanks of the extinct Kisingiri Volcano (Figure 1). The sediments that make up the island accumulated during the Miocene in a graben associated with carbonatite-nephelinite volcanism from the adjacent Kisingiri Volcano. The graben was created during the onset of rifting in the Nyanza Rift System (e.g., Shackleton, 1951; Van Couvering, 1972; Le Bas, 1977; Drake *et al.*, 1988; Bestland, 1991). During the early Miocene, Rusinga would have formed on the outer edge of the central volcanic massif in a crustal depression (Van Couvering, 1972; Le Bas, 1977; Drake *et al.*, 1988; Ebinger, 2005). The Mfangano Fault, which was likely created as a result of Nyanza Rift processes, creates a deep channel between Rusinga and mainland Kenya. Plio-Pleistocene development of the Lake Victoria Basin and the relatively recent filling of the Lake Victoria created the separation of Rusinga Island from the mainland along the Mfangano Fault (see Danley *et al.*, 2012 for review of the geologic history of Lake Victoria).

The early Miocene sedimentary succession on Rusinga is composed of the Rusinga and Kisingiri Groups (Figure 1), with the majority of fossils coming from the older Rusinga Group. Rusinga Group succession consists of pyroclastic, fluvial, lacustrine, and lahar deposits that record active volcanism and periodic landscape stability (Van Couvering & Miller, 1969; Van Couvering, 1972; Le Bas, 1977; Bestland *et al.*, 1995; Bestland & Krull, 1999; Peppe *et al.*, 2009) and is divided into (from oldest to youngest): the Wayando Fm., Kiahera Fm., Rusinga Agglomerate, Hiwegi Fm., and Kulu Fm. (Van Couvering, 1972; Peppe *et al.*, 2009). The Hiwegi Formation has been further subdivided into the Kaswanga Point, Grit, Fossil Bed, and Kibanga members (Figure 1; Van Couvering, 1972; Drake *et al.*, 1988). The younger Kisingiri Group is subdivided into the Kiangata Agglomerate and Lunene Lavas, and comprises thick lahar deposits and capped by a series of lava flows (Figure 1; Van Couvering, 1972; Le Bas, 1977). Although there has been some debate about the order of the stratigraphic units on the island (e.g., Van Couvering, 1972; Drake *et al.*, 1988; Bestland, 1991; Peppe *et al.*, 2009; Michel *et al.*, 2014), recent stratigraphic and paleomagnetic work (Peppe *et al.*, 2009, 2017b) confirmed the basic sequence of formations mapped by Van Couvering (1972) and Drake *et al.* (1988), and made some important changes to the stratigraphic positions of specific fossil sites (Retallack *et al.*, 1995; Michel *et al.*, 2014; Peppe *et al.*, 2017b).

Drake *et al.* (1988) suggested that the Kiahera, Rusinga Agglomerate, and Hiwegi Formations record the early explosive eruptive history of the Kisingiri Volcano, followed by a period of volcanic quiescence during the deposition of the Kulu Formation, and then a thick series of extrusive volcanics in which (on Rusinga Island) the Kiangata Agglomerate is capped by the multiple lava flows of the Lunene Lavas. Alternatively, based on the depositional features of

the deposits on Rusinga, Bestland et al. (1995) argued that the Rusinga and Kisingiri Groups documented up to three cycles of doming and eruption: (1) the Wayando and Kiahera formations represent the first cycle, (2) the Rusinga Agglomerate and lower Hiwegi Formation represent the second cycle, and (3) the upper Hiwegi Formation through the Lunene Lavas represents the third and final cycle. In either scenario, the succession of sedimentary rocks on Rusinga documents the prolonged eruptive history of the Kisingiri Volcano.

Although volcanism persisted throughout deposition of most of the Rusinga Island strata, dating the deposits has been difficult due to leaching and loss of potassium from biotites, inheritance from the Precambrian basement through which that Kisingiri Volcano erupted, and the scarcity of other dateable minerals like sanidines or zircons (Drake *et al.*, 1988; Peppe *et al.*, 2011, 2017b). However, ongoing work using Ar-Ar dating coupled with paleomagnetic analysis has shown potential, and suggests the units on Rusinga are older and represent a longer duration of deposition of the succession than previously thought: from about 20-17 Ma (Peppe et al., 2017a, b).

Fossil material was first identified from Rusinga in a British colonial report on the East Africa Protectorate (Maufe, 1908), and paleontological field work began in earnest in the 1930s through L.S.B. Leakey's East African Archaeological Expedition and later the British-Kenya Miocene Expedition (see Pickford, 1984). Subsequent research by Andrews in the 1970s (e.g., Andrews, 1972; Andrews and Van Couvering, 1975), and by Walker, Pickford, and Teafor in the 1980s (see, e.g., Teafor *et al.*, 1988; Walker & Teafor, 1988; Walker *et al.*, 1993; Walker, 2007) helped contribute to fossil assemblages numbering in the tens of thousands of specimens.

Much of the research on Rusinga was motivated by the discovery there of early fossil apes and other catarrhine primates. Best known among these is the medium-sized ape *Ekembo* (previously referred to *Proconsul*; McNulty et al., 2015), which – due to its extensive anatomical representation as well as its position near the base of the ape-human clade – has figured prominently in studies of hominoid origins (e.g., Le Gros Clark & Leakey, 1950; Napier & Davis, 1959; Pilbeam, 1969; Andrews, 1978; Harrison, 1987; Walker et al., 1993), the evolutionary diversification of later ape (Simons & Pilbeam, 1965; Kelley, 1988; Pilbeam et al., 1990; Begun, 1994; Moyà-Solà & Köhler, 1996; Chaimanee et al., 2004; Alba et al., 2011, 2015), and the origin of the human clade (e.g., Kunimatsu et al., 2007; Lovejoy et al., 2009; White et al., 2009; Almécija et al., 2015). Unique taphonomic assemblages such as Whitworth’s “pothole” (now understood to be an infilled tree trunk; Walker, 1992, 2007) and the Kaswanga Primate Site (Walker, 1992) combine with hundreds of other fossil remains to characterize almost every aspect of the skeleton of *Ekembo*.

A critical aspect of understanding the adaptive evolution of *Ekembo* and Rusinga’s other primates is identifying the habitat or habitats in which they lived. More than 90 species of mammal are now known from the Hiwegi Formation, making it one of the most diverse fossil mammal assemblages in the African Neogene and providing detailed information about the mammal communities from this period. Likewise, a variety of plant remains – including leaves, fruits, nuts, tree trunks, and roots – document the floral component of these early Miocene habitats (Chesters, 1957; Collinson, 1983; Collinson et al., 2009; Maxbauer et al., 2013; Michel et al., 2014).

200 Nevertheless, this rich dataset of plant and animal remains has not resulted in
201 consistent paleoecological reconstructions in Rusinga's sedimentary record. Several researchers
202 have identified the Hiwegi Formation as representing a closed-canopy forest based upon
203 evidence that includes fossil flora (Chesters, 1957), fossil tree-stump casts (Michel *et al.*, 2014),
204 affects of volcanism that biases stable isotope results (Harris & Van Couvering, 1995), and
205 *Ekembo* anatomy and inferred locomotion styles (see discussion in Walker, 1997), among other
206 observations. Alternatively, others have suggested that the environment was open and perhaps
207 semi-arid based on analyses of paleosols (Bestland & Krull, 1999; Forbes *et al.*, 2004). In
208 between these two extremes, a variety of research has concluded that some type of mixed
209 environment was present during deposition of the Hiwegi Formation (Collinson *et al.*, 2009;
210 Ungar *et al.*, 2012; Maxbauer *et al.*, 2013). The varying interpretations likely result from a
211 variety of factors, including time averaging within and among fossil assemblages, biases in the
212 fossil collections, a lack of correspondence between early Miocene and modern species
213 ecologies, inappropriate application of geochemical methods to the paleosols, and the fact that
214 most non-paleontological reconstructions come from sites that have not been correlated to
215 environmental reconstruction, or to the major fossil localities. For example, some paleosol and
216 stable isotope-based paleoenvironmental reconstructions of the Hiwegi Formation suggested
217 an arid environment (Bestland & Krull, 1999; Forbes *et al.*, 2004); however, other researchers
218 suggested that the stable isotope geochemistry was not reliable and should not have been
219 applied to the paleosols. They suggest instead that the aridity signal was one of "mock-aridity"
220 that was a result of high carbonate content of the carbonatite parent material and frequent
221 eruptive activity clearing vegetation (Harris & Van Couvering, 1995). Thus, despite the large

number of reconstructions, the paleoenvironment for the Hiwegi Formation is still relatively poorly understood and requires additional study, particularly work that ties fossil localities and fossiliferous strata to a detailed stratigraphy of the Hiwegi Formation.

3. Methods

3.1 Sedimentology

Field work in 2009, 2010, and 2011 included mapping of stratigraphic units and description and sampling of paleosols from the Hiwegi Formation at R1, R2, and R3 fossil sites (cf. site numbering in Pickford, 1984). Although R2 is not part of the Waregi Hill complex, the presence of a lithological unique marker bed was used to help correlate it with the R1 and R3 sections (Michel *et al.*, 2014). Stratigraphic sections were trenched to expose bedding contacts and fresh bedding surfaces (as well as to remove effects of surficial weathering) and measured to the nearest decimeter using a Jacob's staff and Abney hand-level. Paleosols were described using methods advocated by Retallack (1988) and Tabor *et al.* (2017) based on modern soil description (Soil Survey Staff, 2010; Schoeneberger *et al.*, 2012), and included ped size and structure, paleosol-horizon boundary conditions (i.e. degree of smoothness and distance of horizon change), degree of calcareousness, and Munsell color. Paleosol B-horizons were sampled for clay mineralogy, and samples were painted in the field with polyester resin before being chiseled out and wrapped in aluminum foil for preparation for micromorphological analysis.

3.2 Laboratory

Thin sections of ped samples were made by Spectrum Petrographics, Inc. (www.petrography.com) thin-section preparation, followed by micromorphological analysis to determine the extent of weathering of primary minerals. Thin sections were examined at Tennessee Technological University using a Leica research microscope, and subsequently described using standard soil micromorphological techniques (Bullock *et al.*, 1985; Stoops, 2003; Stoops *et al.*, 2010). Clay mineralogy was determined through disaggregating the fine matrix in deionized water and isolating the <2 μ m equivalent spherical diameter (e.s.d.) size fraction through centrifugation. The <2 μ m fraction was used to create oriented aggregates using established methods (Moore & Reynolds, 1997) including a four-step salt solvation (Jackson, 1969). Mineralogy was characterized using a Siemens D5000 Θ -2 Θ X-ray diffractometer at Baylor University with Cu-K α radiation over 2 to 30° 2 θ , a step scan of 0.04, and a dwell time of 1 second. Peak shifts were then examined to determine clay mineralogy based on methods outlined in Moore and Reynolds (1997). Internal standards of pure clay minerals were periodically run for quality control.

3.3 Paleontology

Fossil collection at site R1 by our team began during the first survey trip to Rusinga in 2006 and continued annual between 2006-2013 and again from 2016-present. The first preliminary survey of R3 by our team was conducted in 2008 with additional collecting from 2009-2013 and in 2016-present. For surface collections, identifiable fossils were collected by a team walking side by side in a line following a pattern to cover the whole site systematically. Small fossiliferous outcrops were bagged separately and associated with GPS coordinates;

individual specimens were later recorded and stored in their own collecting bags in camp. In addition, each site was surveyed for one field season using a more rigorous protocol to record and digitize fossil distributions. In these seasons, every bone fragment larger than 2 cm, as well as every diagnostic anatomical element (teeth, joint surfaces, etc.), was flagged and left in place. Each flag position was then recorded using either a Trimble differential GPS (2010) or a Total Station (2011). Fossils collected during these seasons are each associated with high-resolution provenance information.

In addition to surface collections, we also report one gridded excavation at an area within R1 that had exceptionally dense fossil deposits. That site, informally dubbed “Rodent Hill,” was located in the northeastern half of R1 at coordinates UTM 36 M 0634835 9955153 (datum: WGS 84). All sediments around the site were surface swept and screened and a 24 m² grid was established for excavation. Fossils found *in situ* were piece-plotted on a map and all excavated sediments were screened using successive 5.0 mm, 2.0 mm, and 0.5 mm sieves followed by wet-sieving. Units were excavated in arbitrary 5 cm levels within clear stratigraphic layers.

All fossils reported in this study were identified to the lowest taxonomic level possible and to anatomical element based on comparisons with collections at the National Museums of Kenya and published literature. The number of individual specimens (NISP) was calculated to measure taxonomic structure and composition of the collected fauna (Lyman, 2008). We generated multiple faunal lists for the Hiwegi Formation at Waregi Hill based on available provenance data for the specimens (Table 1). Specifically, we included separate faunal lists for R1 and R3 that summarize the entirety of our collections since 2006 (“All”), and we compare

them to lists from the historic collections as reported by Pickford (1986) (Table 1). In addition, R1 has a faunal list for the stratigraphically-controlled excavation at “Rodent Hill” (Table 1). Likewise, the R3 site has separate lists for specimens found in association with the “forest paleosol” (Michel et al., 2014) and those found in a ravine at the north end of R3 (Table 1), which is stratigraphically lower than the paleosol. These two fossil horizons at R3 are separated by a resistant siltstone that dips in a southerly direction, and hence surface-collected fossils from the forest paleosol can be separated from the older ravine fossils because the former erode in the opposite direction from the ravine. The site-wide faunal lists (Table 1) combine fossils that were surface-collected without further stratigraphic information, and likely record a time- and stratigraphically-averaged faunal signal for each site. Given the large number of specimens recovered historically, the site-wide collections (Table 1) represent a good sample of the overall conditions that prevailed during the time of accumulation (Olszewski, 1999), and can be used in broad comparisons between other sites on the island. However, they cannot be used to resolve fine-scale questions about the paleoenvironment or paleoclimate of the time, or to assess patterns of faunal change through the Hiwegi Formation.

4. Results

4.1 Sedimentology

The Hiwegi Formation at Waregi Hill is represented by ~57 m of section, and can be further subdivided into Grit, Fossil Bed and Kibanga members (Van Couvering, 1972). The lowermost Kaswanga Point Member does not crop out at Waregi Hill (Van Couvering, 1972). The formation is underlain here by the Ombonya Beds, a geographically constrained geologic

unit found only at Waregi Hill, and unconformably overlane by the Kiangata Agglomerate and Lunene Lavas (Van Couvering, 1972; Walker & Pickford, 1983). As the Ombonya Beds, Kiangata Agglomerate, and Lunene Lavas lack both fossils and paleosols; they are not discussed here. The Hiwegi section includes 11 distinct paleosols (P1-P11; Figure 2) within or above the R1 fossil site. The R3 site is north of the main Waregi Hill section, and can be linked to the upper portion of the R1 section via tracing of key marker beds and lithologic correlation.

At Waregi Hill, the Grit and Fossil Bed members comprise the lower 25 m of the Hiwegi Formation, and across Rusinga the two members were dominated by debris-flow, sheet-flow or flash-flood processes, operating in periodically active channels. Sediments were deposits within channels and on adjacent floodplains and local evaporitic ponds. These fluvial and ponded deposits have evidence for variable flow and evaporative conditions and are intercalated with variably weathered airfall tuffs and paleosols (Figure 3A). The deposits have abundant sedimentary structures indicating lower and upper-flow regimes and variable flow, including finely laminated siltstones, cross-stratified and rippled silt and sandstones, laminated fine- to coarse-grained sandstones, normally graded bedding, and they scour into the underlying stata. Thicker conglomerates and coarse grained sandstones with no sedimentary features also occur in these units. Evaporitic desiccation and dewatering sedimentary structures, including mud cracks, flame structures, salt hoppers, tepee structures, and satin-spar calcite after gypsum are relatively common within and on the tops of bedding planes (Figures 3B, 4). Given that there are no sedimentological differences between the Grit and Fossil Bed members as described by Van Couvering (1972), and that the only difference between the units is the presence of fossils, we report their results together.

332 The Grit and Fossil Bed members are easily distinguished from the overlying Kibanga
333 Member, which is dominated by bedded airfall tuff deposits (Figure 3D). The bedding in the tuff
334 deposits ranges in thickness from a few centimeters to >10 cm thick (Figure 2, 3D). Tuff
335 deposits comprise a mixture of ash, accretionary lapilli, volcanic breccia blocks and bombs, and
336 abundant biotite mica flakes. Generally, these deposits are tuff breccias comprised of volcanic
337 clasts primarily ranging from fine-sand to fine-gravel in size, although lapilli tuffs, which are
338 dominated by accretionary lapilli and volcanic clasts smaller than fine sand, are also common.
339 These beds mostly have no sedimentary structures, though some are normally graded. Breccias
340 and conglomerates with abundant subhedral to angular biotite mica grains up to ~2-5 cm in
341 diameter with no sedimentary structures occur between the air-fall tuff deposits. These beds
342 range from a few cm to >1 m thick and likely represent volcanoclastic deposits that were
343 remobilized and redeposited by debris flows. Interspersed within these volcanic deposits are
344 fluvial deposits, which are a mixture of normally graded to massive polymictic conglomerates
345 and breccias, fine- to coarse-grained cross-laminated to laminated sandstones, thinly bedded
346 siltstone and mudstones, and heterolithic flaser beds. The conglomerates are laterally
347 heterogenous, with a coarse-grained sandstone matrix and granules to fine pebbles; however,
348 in some places there are groups of larger cobbles. Most of the conglomerates contain a blue-
349 green matrix and always incise into the underlying strata. These fluvial deposits were likely
350 deposited via sheet flows and in periodically active channels and on their adjacent floodplains.
351 The tops of several of the airfall tuff, reworked volcanic, and fluvial deposits are pedogenically
352 modified. The Kibanga Member comprises the upper 32m of the Hiwegi Formation at Waregi
353 Hill.

354

355 *4.1a Grit/Fossil Bed Member paleosols*

356 The Grit/Fossil Bed Member contains seven paleosols (labeled P1-P7; Figure 2) at
357 Waregi Hill. Near the base, P1 is a moderately formed Calcic Protosol (sensu Mack *et al.*, 1993)
358 characterized by a single horizon with evidence of stage II carbonate nodules (Gile, 1961;
359 Machette, 1985) (Figure 3A). The paleosol has subangular blocky structure and weak soil
360 development. Clay mineralogy of the paleosol is dominated by smectite and illite.
361 Micromorphology of the lower deposits reveals basalt clasts altering to Fe-Mn oxides or
362 exhibiting alteration rinds (Figure 5A, B). Micritic carbonate is not uncommon but has textures
363 unusual for pedogenic carbonate, including inclusions of silicate minerals such as quartz (Figure
364 5 C, D) and weathering rinds rimming the nodules (Figure 5C).

365 Above P1 are 10 m of sandstones and conglomerates, which have not been strongly
366 pedogenically modified though there is evidence of weathering rinds of clay on some of the
367 lapilli. Between 18 and 20 meters within the section are four separate siltstones with antiformal
368 “tepee structures,” satin-spar calcite pseudomorphous after gypsum (Figure 3), and
369 birefringent fabric (B-fabric) and oriented clay (Figure 4). Locally, the uppermost siltstone is
370 laterally extensive and was used as a correlative unit mapped throughout R1. These siltstones
371 with satin-spar calcite after gypsum are interpreted to represent local evaporitic pond deposits.

372 Above the siltstone marker bed are four very weakly developed, noncalcareous
373 paleosols (P2-P5), which exhibit subangular blocky ped structures and have drab-haloed root
374 traces. Their clay mineralogy is composed of smectite and illite. The upper two paleosols in the
375 Fossil Bed Member (P6 and P7) are sandy siltstones with a system of large calcified root traces

(Figure 3C). However, they lack evidence of fossil tree stump casts, such as those documented in paleosols of the Kibanga Member (Michel et al., 2014). Micromorphology of thin sections from paleosols P2-P7 confirms field observations of weak soil development including weathered volcanic rock fragments, the presence of biotite and pyroxene (5E, F); highly reactive volcanic glass is relatively unaltered and visible in thin section (Figure 5G). Lapilli fragments in various states of weathering are common as matrix material. Some of the lapilli have been completely weathered and carbonate (either micrite or spar) has infilled the secondary pore space. Sericitized feldspars, with rare sparry calcite cement encircling the grains (Figure 5H) are seen in thin section. There is weak development of pedality and no evidence of biological structures (i.e., no rhizoliths, bee brood casts, insect burrows) seen in thin section. Fe-Mn oxides occurs as dendritic growths (Figure 5E, F) in both the paleosols and fluvial deposits. Although all of the Grit/Fossil Bed Member paleosols are relatively poorly developed, micromorphology indicates a trend toward increased weathering and better soil development, from the bottom to the top of the member.

4.1c Kibanga Member Paleosols

There are four weakly developed paleosols within the Kibanga Member (P8-P11) classified as Protosols. Clay mineralogy of all of the paleosols in the Kibanga Member is smectite and illite. Two paleosols (P8 and P9) occur in the lower half of the Kibanga Member and a few other beds in this interval show weak weathering indicating incipient soil development. P8 and P9 have weak angular blocky to vertic ped structure, and two of the lowermost stratal units with incipient soil development contain drab-haloed root traces. Both

paleosols also contain carbonate, but it is difficult to determine in the field whether these are calcified root traces (Figure 3F) or pedogenic nodules (Figure 6A). Micromorphology confirms evidence of weak weathering, which is evident from the presence of abundant volcanic minerals such as hornblende, sericitized feldspars, and biotites. Surprisingly, although many of the volcanic rock fragments are unweathered, most of the accretionary lapilli have been weathered to clay or calcite (Figure 6B). The calcite in thin section occurs both as micrite and spar (Figure 6A). In three of the four paleosols, there is no evidence of biological activity and only weak, if any, development of ped structure or B-fabric observed in thin section.

The tenth paleosol (P10) occurs at 48 m in the Waregi Hill section in the Kibanga Member and is well exposed at R3. This paleosol preserves infilled fossil tree trunk casts and root casts (Michel *et al.*, 2014), and is characterized by a coarse texture, weak subangular blocky to massive soil structure and color ranging from dark grayish-brown (10 YR 4/2) to reddish brown (2.5 YR 5/3). The paleosol is cumulic and consists of multiple fining-upwards successions and changing colors that are aggregated into a single Bw horizon. The matrix varies from highly calcareous to noncalcareous, and is calcite-cemented in the basal horizon. This paleosol occurs at multiple localities (R1, R2, and R3 in Figure 1; for more detail, see Michel *et al.*, 2014), and shows little variation in field characteristics where it has been documented. This paleosol overlies a conglomerate that is characterized by a red matrix and contains diorite clasts, which is unique within the entire Hiwegi Formation. The conglomerate was used as a marker bed to correlate the stratigraphy associated with this paleosol at all three localities (R1, R2, and R3). We found varying degrees of incision into the paleosol by an overlying sandstone, which has a blue matrix with clasts that range from granules to cobbles. Well-preserved fossil

420 leaves occur on thin mud drapes near the base of the sandstone bed (Michel et al. 2014). Tree
421 stump casts were identified not only at R3, but also in the correlative stratigraphic sections
422 above R1 and at R2 (Michel et al., 2014), and calcite-cemented root casts were also found at R3.
423 The root casts show many different macromorphological patterns, including branching and
424 tapering, which are characteristic of modern roots (Michel et al. 2014). Clay mineralogy reveals
425 a clear trend with depth. At the surface of the paleosol across all sites both smectite and illite
426 are present, as well as quartz in the <2 μ m clay fraction; at depth only illite and quartz are
427 present.

428 Micromorphological analysis of P10 reveals evidence for weak weathering of detrital
429 grains of feldspars, pyroxenes, and volcanic rock fragments. This is the only paleosol in the
430 Kibanga Member in which there is strong evidence of biological processes observed in thin
431 section, including abundant bee brood casts (Figure 6C), termite termitaria (Figure 6D), root
432 casts, and fossilized oribatid mite fecal pellets (Figure 6E). There is no development of B-fabric,
433 and in only one thin section was there evidence of illuviated clay (Figure 6G). One of the
434 calcite-cemented root casts was characterized both macromorphologically and in thin section,
435 and it shows internal structures characteristic of modern roots, including differentiation into
436 distinct tissues (e.g., phloem and xylem) as evidenced by different textural properties of infilling
437 materials. This suggests that decay of different plant tissues occurred at different stages (see
438 Figure 3e in Michel et al., 2014). All pore space has been cemented by an inclusive calcite
439 cement that included siliciclastic grains, and luminesces strongly red when viewed under CL.
440 Secondary pore space from weathering of volcanoclastic materials was subsequently infilled by
441 Fe-Mn masses.

Above the P10 forest paleosol are sandstones, some of which show pedogenic overprinting including evidence of root traces and weathered volcanic ashes. One of these weathered ashes is a weakly developed Protosol (P11) with conchoidal fracture to weak angular blocky structure. Micromorphology reveals lapilli that have weathering rinds of oriented clay (Figure 6F). However, there is no strong evidence of rooting or other pedogenic features such as carbonate nodules.

4.2 Paleontology

A revised mammalian faunal list for the Hiwegi Formation is presented in Table 1, based on data from Pickford (1986), Werdelin & Sanders (2010) and our own collections since 2006. Almost 600 fossil mammal specimens from our (2006-present) collections at R1 and R3 were sufficiently well-preserved to identify at the genus level (Table 1). Several additional taxa from both sites are reported at higher taxonomic levels or as possibly but not definitively present, but these are not included in comparisons below.

The taxonomic composition at R1 of surface collections combined with the “Rodent Hill” excavation include 40 identified genera; surface collections at R3 yielded 22 identified mammalian genera. Twenty-one of the 22 R3 genera are also found at R1, the exception being a new genus of gomphothere (B. Sanders, personal communication). Comparisons of our R1 collections (Table 1: “R1 ALL”) with historic collections compiled by Pickford (1986) reveal broad similarities: 40 vs. 37 genera identified, respectively; the Jaccard similarity coefficient and Sørensen–Dice index (Lyman, 2008) between our and historic collections were 0.51 and 0.67, respectively, which suggests an average match between the lists. At R3, however, we found

considerably fewer genera compared to the previously collected assemblages. Thirty-eight genera are known there historically whereas we identified only 22 genera in our collections; likewise, the same faunal indices are low (Jaccard: 0.36; Sørensen–Dice: 0.53), indicating important differences between collections (Table 2). The number of specimens identifiable to the genus level for our “R3 ALL” collection (fewer than 200 specimens vs ca. 400 for “R1 ALL”) could explain this discrepancy, as both similarity indices are sensitive to differences in sample size (Magurran, 2004). Moreover, the greater extent of fossil exposure and corresponding time spent at R1 is much higher than at R3. Nevertheless, the near absence of Carnivora, Hyainodontidae, Tenrecidae and Macroscelidae in our R3 collection compared to historical collections is striking (Table 1).

Pickford’s (1986) faunal lists for R1 and R3 share 33 genera and have only five unique genera each. The elevated Jaccard similarity coefficient and Sørensen–Dice index (0.77 and 0.88, respectively) confirm the high similarity between these lists. Conversely, the similarity indices of our collections indicate considerable differences between the R1 (ALL) and R3 (ALL) faunal lists (0.37 and 0.54, respectively) (Table 2). These differences are also evident when considering the subsets of collections at the different sites (see Table 2). For instance, the R3 “ravine” collection shows a different taxonomic composition than the R3 “forest paleosol” collection, and the microfauna-dense R1 “Rodent Hill” collection differs from the overall collection made at R1. These differences may reflect taphonomic biases and/or real differences in faunal occurrences spatially and temporally.

Based on our collections, mammal communities at R1 and R3 are both dominated by small-sized animals (e.g., rodents, lagomorphs, elephant shrews), but with important

differences in the occurrences and abundance of specimens. The R1 fauna is especially dominated by specimens of the small artiodactyl genus *Dorcatherium* (30.5%) (Table 3). This is also true at the microfauna-dense R1 “Rodent Hill” site, where *Dorcatherium* represents almost half of the identified specimens. In contrast, *Dorcatherium* represents only 15.5% of the mammal specimens at R3, and is only the second-most abundant genus. The cane rat, *Paraphiomys*, is the most abundant rodent genus found at R1 and R3 (Table 3). However, specimens of *Diamantomys* are much more common at R3 than at R1 (13% vs 2.7% respectively), suggesting that rodent community structures differed considerably between sites. Lagomorphs (genus *Kenyalagomys*) are found in similar abundances, carnivorous mammals are rare, and tenrecs are almost absent at both sites. Elephant shrews occur at R1, but not R3. Hence, the taxonomic abundance for each genus differs significantly between R1 (R1 “ALL”) and R3 (R3 “ALL”) (chi-square = 70.28; $p < 0.01$). However, abundances of genera are correlated between R1 and R3 (Spearman’s rho = 0.52; $p < 0.01$), suggesting that the most abundant genera are the same in both sites, albeit with differences in the rank of abundance.

Among larger mammals, only the cursorial large hyraxes (*Afrohyrax*) are relatively abundant at both sites, though they are more common at R1 than at R3. Interestingly at R3, *Afrohyrax* was only found in the “forest paleosol,” even though it is more typically thought to represent an open-adapted taxon (Whitworth, 1954). Proboscideans are rare in both sites, but it is worth mentioning that, with reference to the Waregi Hill outcrops, gomphotheriids have only been found in the “forest paleosol” at R3, adding to the body of evidence that this lineage first favored C₃ vegetation (or browse) before exploiting C₄ grasses (i.e., more open environments) in the later Neogene (Cerling *et al.*, 2005).

508

509 **5. Discussion**510 *5.1 Stratigraphy*

511 Through the Hiwegi Formation at Waregi Hill there are differences in mechanisms of
512 deposition between some stratigraphic members. However, contrary to Van Couvering (1972)
513 and to subsequent references to this formation (e.g., Pickford, 1984; Drake *et al.*, 1988; Peppe
514 *et al.*, 2009), we do not find significant depositional, lithostratigraphic, or sedimentological
515 differences between the Grit and Fossil Bed Members and hence group them together here.
516 The Grit/Fossil Bed Member is dominated by fluvial and ponded deposits and poorly developed
517 paleosols. In contrast, the Kibanga Member is dominated by volcanic deposits (air-fall tuff and
518 reworked tuff) intercalated with fluvial deposits and paleosols. Thus, we interpret the member
519 contact between the them to represent a change from fluvially dominated deposition
520 (Grit/Fossil Bed Member) to volcanically dominated deposition (Kibanga Member). This was
521 likely driven by an increase in the number, duration, proximity, and/or size of eruptive events of
522 the nearby Kisingiri Volcano, as well as changes in climate through time, which is discussed in
523 more detail below.

524

525 *5.2. Paleoenvironment and Paleoclimate of the Hiwegi Formation*

526 The sedimentology of the deposits and macro- and micromorphologic analyses of the
527 paleosols at Waregi Hill indicate that the Hiwegi Formation represents a dynamic landscape
528 that transitioned from drier and more open habitats where evaporation exceeded precipitation,
529 to wetter and more closed habitats in which dense, closed-canopy forests developed.

530 Additionally, there is strong evidence for seasonality, or at minimum, episodic precipitation
531 through the entire Formation.

532 During deposition of the basal part of the Hiwegi Formation, there is strong evidence for
533 a dry, seasonal climate in which evaporation exceeded precipitation. Except for scoured bases,
534 the sandstones, conglomerates, and breccias in the lower 25 m of the Grit/Fossil Bed Member
535 at Waregi Hill have relatively limited evidence for channel-forms, and many of the horizontally
536 laminated and cross-bedded strata are laterally extensive suggesting that they represent sheet-
537 flood deposits deposited during episodic rainfall events. In these layers, the fossils were likely
538 deposited after being washed in from the floodplains during flooding (Stear, 1985). Deposits
539 with more clear channel features commonly are horizontally-laminated or cross-bedded, show
540 normal grading, and are scoured at the bases, which suggests variable reactivation of bedforms
541 and subsequent deposition, likely triggered by episodic precipitation events. Although the first
542 paleosol is a moderately developed Calcic Protosol *sensu* Mack et al., (1993), the rest of the
543 paleosols (P2-P5) within this interval are poorly developed (possible Calcic Protosols or
544 Protosols) and retain abundant unweathered volcanic fragments, suggesting relatively little
545 weathering that is perhaps due to limited rainfall. Given the poor paleosol development, there
546 are limited interpretations one can make for them. However, the presence of pedogenic
547 carbonate and/or satin-spar calcite pseudomorphous after gypsum in some of these paleosols
548 and/or sediments is evidence for an environment in which evaporation exceeded precipitation
549 (e.g., Amit & Yaalon, 1996; Deutz *et al.*, 2002; Buck & Van Hoesen, 2005; Breecker *et al.*, 2009).
550 Between P1 and P2 are four discrete siltstone beds with tepee structures and abundant satin-
551 spar calcite pseudomorphous after gypsum. Given their evaporitic features, the distribution of

these deposits and their characteristic antiformal shape in outcrop exposures, we interpret the siltstone beds to represent evaporitic ponds that likely became hypersaline, allowing gypsum to precipitate, something that is common today in highly evaporitic environments (Watson, 1979, 1985, 1988, 1992).

Interestingly, magnetostratigraphy of the Hiwegi Formation (Peppe *et al.*, 2017b) indicates that the siltstone beds and paleosols P2-P5 at Waregi Hill correlate to a fossiliferous interval at R5 (Kaswanga Point) where there is also evidence for evaporitic conditions (Conrad *et al.*, 2013; Maxbauer *et al.*, 2013). This includes a rippled sandstone unit with abundant fossil leaves that is capped by a bed with mud cracks and salt hoppers on the top of the bedding plane, indicating subaerial exposures and evaporitic conditions (Maxbauer *et al.*, 2013). This unit at R5 is overlain by 10 meters of fluvial deposits with interbedded paleosols, which correlate to stratigraphic intervals at Waregi Hill in which paleosols P2-P5 occur. The R5 paleosols and fluvial deposits also show evidence for an environment in which evaporation exceeds precipitation, including pedogenic carbonate in the paleosols and mudcracks on the tops of many bedding planes.

Fossil leaves from R5 suggest that the climate was relatively warm, and that the vegetation sampled a riparian habitat of woodlands and forest (Maxbauer *et al.*, 2013). Likewise, analyses of flora from R117, which samples a similar stratigraphic position to the R5 flora, indicated that the local paleoenvironment was a woodland with limited forest in the area (Collinson *et al.*, 2009). Taken together, these distinct sources of information point to evaporitic conditions within the lower Grit/Fossil Bed Member that were not locally restricted and to a climate during this interval that was seasonal.

The upper two paleosols in the Grit/Fossil Bed Member (P6 and P7) have similar macro- and micromorphologic features to the paleosols P1-P5; however, they are slightly better developed, albeit still Protosols. Additionally, they have abundant large carbonate nodules, which appear in outcrop cross-section to be stage II pedogenic carbonate. However, excavation of these nodules indicate that they are carbonate cemented root casts (Figure 3C) that are up to 283 cm long and 9.5 cm wide. Although these paleosols' horizons lack tree stump casts, these carbonate-cemented root casts are interpreted as belonging to trees. The abundance, thickness, and length of the root casts imply a more closed environment. However, without preserved tree stump casts it is currently impossible to determine whether this represented a dense patch of trees on the landscape within a broader, more open habitat or were part of a more closed forest. These paleosols and the surrounding fluvial deposits have minimal evidence for evaporitic conditions, in contrast with older P1-P5 paleosols. Taken together, the occurrence of tree root casts, which potentially suggests a more closed environment, the increase in weathering, and the absence of evaporitic indicators suggest that the upper Grit/Fossil Bed Member likely sampled an environment that was becoming more closed as a result of increased precipitation.

Within the Kibanga Member, paleosols P8 and P9 are also Protosols. Similar to paleosols P6 and P7, these appear to contain stage II pedogenic carbonate, which have only been found in cross-section of the outcrop, with no place to easily dig in to assess their morphology. Given the similarity of these nodules to the carbonate-cemented root casts in P6 and P7, we speculate that these nodules are also mostly likely calcified root casts that were associated with trees.

596 The next paleosol in the Kibanga Member, paleosol P10, is a Protosol containing
597 abundant tree stump casts and calcified root systems, which was described by Michel et. al
598 (2014) from exposures at R3 with additional data from R1 and R2. Mapping of the tree stump
599 casts from this unit indicate the presence of a closed-canopy forest in this interval.
600 Macromorphological features and grain-size analysis of P10, which show multiple fining-
601 upwards sucessions, indicate that this interval samples a dynamic, active volcanic environment
602 in which there was regular and continued input of volcanic ash. Micromorphologic features
603 suggesting well-drained conditions (e.g., illuviated clay, bee brood casts) and intervals of poor
604 drainage (e.g., Fe-Mn masses and depletions), when taken together, suggest a seasonal
605 precipitation regime. Although there is illuviated clay present in thin sections, it is rare, and
606 the dominant weathering reaction that has occurred has been the alteration of highly reactive
607 volcanic glass to clay. This lack of abundant illuviated clay and the presence of metastable
608 volcanic rock fragments and weatherable minerals, such as plagioclase feldspar and pyroxenes,
609 indicate either a relatively short duration of pedogenesis or a dry climate in which very little
610 water passed through the soil system. The clay mineralogy also indicates the lower end of the
611 spectrum of weathering intensity, with illite present throughout the soil profile and smectite
612 present only in the upper part of the soil horizon. Illite and smectite are early weatherable
613 minerals in felsic igneous rocks, with smectitic clay found when precipitation is less than 100
614 cm/yr (Barshad, 1966; Birkeland, 1999). Fossil leaves from the bed directly above P10 suggest
615 a warm and relatively wet climate.

616 Retallack et al. (1995) and Bestland et al. (1995) also described paleosols from the
617 Waregi Hill section and from R3, and our results are somewhat similar. However, both previous

studies recognized considerably more paleosols in their Waregi sections than are reported here; in many cases the paleosols they described were characterized as weakly developed, consisting only of an A or C horizon. A more conservative approach was taken here, describing only paleosols that had good horizonation (i.e., a B horizon) and that could be used for paleoenvironmental reconstructions. For example, in numerous deposits lapilli showed weathering rinds, which could represent possible C horizons. However, unlike Retallack et al. (1995) and Bestland et al. (1995), these types of deposits were not described here because little paleoenvironmental information can be recovered from paleosols with this degree of weathering. In addition, whereas Retallack et al. (1995) described a fossil tree stratigraphically above the forest paleosol we identified here and in Michel et al., (2014) no additional paleosols were identified with evidence of tree stump casts above the fossil forest at R1.

Features of the paleosols and the non-volcanic deposits in the Kibanga Member suggest a wetter climate than the Grit/Fossil Bed Member. Interestingly, Thackray (1994) documented the occurrence of a fossil nest of sweat bees from a paleosol in the Kibanga Member. We cannot verify whether or not this nest was found in a deposit that correlates to one of the paleosols described in this study, but based on geologic maps, the description of the paleosol, and stratigraphic figures in Thackray (1994), the nest was definitely found within the Kibanga Member. A comparison with modern species suggests that soil moisture requirements of sweat bees point to a subhumid to humid climate (see Thackray, 1994 and references therein) – similar to the interpretation for the Kibanga Member presented here.

The climate of the Hiwégi Formation varied from relatively dry and open, in which there was at least seasonal or episodic evaporitic conditions in the Grit/Fossil Bed Member, to a

wetter and more closed habitat in the Kibanga Member. This change over time may help explain variation among paleoenvironmental interpretations in prior studies. In particular, studies that combined fossils from the entire Hiwegi Formation did so using material that lived in dramatically different environments (e.g., Chesters, 1957; Andrews, 1973; Andrews & Van Couvering, 1975; Andrews *et al.*, 1979; Evans *et al.*, 1981; Ungar *et al.*, 2012). Further, studies of restricted stratigraphic intervals (e.g., Thackray, 1994; Collinson *et al.*, 2009; Maxbauer *et al.*, 2013; Michel *et al.*, 2014) did not sample the full range of environments that occurred through the Hiwegi Formation. These results demonstrate that previous studies that treated all fossils from the Hiwegi Formation as coming from contemporaneous environments need to be reevaluated because the studies created time-average assemblages sampling very different environments.

5.2 Paleontology

The fauna collected by us from R1 (Grit/Fossil Bed Member) and R3 (Kibanga Member) differ in both taxonomic composition and abundance. Yet a simple tally of their most abundant taxa reveals nearly identical lists. There are several hypotheses that could explain this result, but given the paleoenvironmental results presented here, the faunal data are interpreted as indicating that different environments throughout the Hiwegi Formation were not individually exclusive of Rusinga's most abundant taxa. This has already been demonstrated for the well-studied fossil catarrhine primates on Rusinga, which appear in a variety of habitats (cf. Retallack *et al.*, 1995; Peppe *et al.*, 2009; Maxbauer *et al.*, 2013; Michel *et al.*, 2014). In fact, the environmental signal in Rusinga's faunal communities is likely not evident in the faunal lists, but

rather in the proportions of taxa found in different habitats. For example, the greater proportion of *Diamantomys* may be an important indicator of a more closed environment, consistent with its dominance at the Tinderet fossil localities (Pickford & Andrews, 1981; Andrews *et al.*, 1997; Andrews & Kelley, 2007). Likewise, the differential abundance of *Dorcatherium* may be important, and having a more robust alpha-taxonomy of these specimens and their proportions may yield a better environmental signal (cf. Ungar *et al.*, 2012).

A further consideration is potential geographic mixing of collections, particularly at R1 where many of the fossil deposits were collected from units interpreted to be channel or flash-flood sheet-flow deposits distributed across a collecting area ca. 0.5 km long. Even if the Grit/Fossil Bed Member paleosols and sedimentary deposits at Waregi Hill represent more open habitats, stream deposits could nevertheless carry in remains from contemporaneous woodland or forest habitats on the volcanic slope, resulting in increased similarities between R1 and R3 faunas. Future taphonomic analyses should help to clarify this issue.

Finally, it seems remarkable that carnivorous mammals, tenrecs, golden moles, and elephant shrews are absent (or nearly so) from our collections at both sites, despite being represented in the historical collections (Pickford, 1984, 1986). In this regard, several authors have pointed out specific cases of unreliable provenience in the historic collections (Leakey, 1967; Andrews & Molleson, 1979; Kelley, 1986). Given the traditional view that R1 and R3 were penecontemporaneous (see, e.g., Van Couvering, 1972), it may be that some collections from the two sites were mixed. Hence, we favor the taxonomic comparisons based on our collections, despite the smaller sample sizes, because the precise location and stratigraphic position of the fossils are known for those collected since 2006. Our collections indicate

notable differences between the R1 and R3 faunas, which suggest that the environmental changes through the Hiwegi Formation likely caused the differences in occurrence and abundance of taxa between R1 and R3.

5.3 Regional comparisons of climate and implications for ape evolution

There has been a significant amount of research on the paleoenvironments of the late Oligocene and early Miocene in East Africa since the 1970s demonstrating a variety of habitats across Africa (e.g., Andrews & Van Couvering, 1975; Axelrod & Raven, 1978; Feakins & DeMenocal, 2010; Jacobs *et al.*, 2010). Nonetheless, it continues to be suggested that during the early Miocene there was a “pan-African” lowland forest that transitioned to a mixture of more open and more closed habitats in the middle Miocene (e.g., Wichura *et al.*, 2015). The pervasiveness of this concept may be due to the fact both historical (i.e., Chesters, 1957; Hamilton, 1968) and recent work has demonstrated considerable evidence for forested environments in East Africa. For example, Oligo-Miocene sites in Ethiopia have been reconstructed as moist tropical forests (Jacobs *et al.*, 2010, 2015; Pan *et al.*, 2012), the Oligo-Miocene of the Turkana Basin was interpreted to be a mosaic environment of semi-deciduous forests and woodlands (Vincens *et al.*, 2006), some of the the early Miocene Tinderet localities were likely forested (Oginga *et al.*, 2017), and there is evidence for a dense closed-canopy forest in a discrete interval in the Hiwegi Formation on Rusinga Island (Michel *et al.*, 2014). Further, the lack of long-term paleoenvironmental records from individual sites makes it easier to argue for a uniform transition from one vegetation type to another.

The high-resolution reconstruction of environments in the Hiwégi Formation presented here demonstrates a strong local habitat signal that changes through time in the opposite direction from that predicted by the “pan-African forest” model. Specifically, results from Waregi Hill depict a transition from more open environments, in which precipitation was seasonal and evaporation considerably exceeded precipitation for at least part of the year, to more closed, forested environments where precipitation was seasonal but considerably higher. Coupled with previous studies from the late Oligocene – early Miocene (e.g., Kingston *et al.*, 1994; Retallack *et al.*, 1995; Jacobs *et al.*, 2010; Maxbauer *et al.*, 2013; Driese *et al.*, 2016; Lukens *et al.*, 2017), the emerging picture suggests that whereas there may have been periods of large forests covering Africa around the time of the Paleogene-Neogene transition, there were also more open regions that varied spatially and temporally due to local conditions, such as topography, differences in local climate, and long-term change in climate. Further, it is likely that even within forested environments there were probably discrete periods when the forest was more open and more closed. The combination of opening and closing forested environments through time and a spatial mixture of more open bushland/woodland and forested environments during the late Oligocene and early Miocene would have caused the repeated breakup and reconnection of forested environments across equatorial Africa. These results supports the hypothesis of Couvreur *et al.* (2008) that repeated forest fragmentation during through the late Oligocene and Miocene created the diverse and highly endemic rainforests seen across Africa today.

The importance of reinterpreting the traditional hypothesis of a “pan-African forest” in the early Neogene was recently proposed (Linder, 2017), and is underscored by results

presented here and by recent evidence of more open conditions from early Miocene Kenyan localities at Karungu (Lukens *et al.*, 2017) and Loperot (Liutkus-Pierce *et al.*, 2019). Early Miocene habitats across Africa were a mixture of more open and more closed environments, somewhat similar to African environmental diversity today (e.g., White, 1983). This calls into question evolutionary scenarios which depict early ape adaptations as arising within closed forest habitats. As Andrews (2016: xiv) notes: for apes, “there was no ‘departure from forest to savanna’, for the primary adaptation of most apes was not to forest in the first place.” With an increasing body of evidence locating early fossil apes and closely related catarrhines outside of forested environments at localities such as Rukwa (Stevens *et al.*, 2013), Karungu (Lukens *et al.*, 2017), Rusinga, Loperot (Liutkus-Pierce *et al.*, 2019), and West Turkana (Butts, 2019), the idea that hominoid origins and early diversification was tied to arboreal adaptations – such as those found in extant apes – may need to be reconsidered.

Conclusions

Deposits from the Hiwegi Formation at Waregi Hill on Rusinga Island in Lake Victoria, Kenya reveal temporal heterogeneity in habitats. Lower in the Grit/Fossil Bed Member there is evidence for variable flow deposits including heterolithic bedding, and widespread sandstone bodies interpreted as sheet-flood deposits. This environment would have been characterized by climatic conditions in which evaporation was much greater than precipitation, based on abundant evidence for evaporite deposits. This semi-arid to arid, possibly seasonal climate created a more open environment of woodlands and riparian forests. This contrasts with the upper Grit/Fossil Bed and Kibanga members, which contain paleosols with slightly stronger

weathering and abundant root and tree stump casts. Fossil leaves, tree stump casts, and calcified root casts cited in previous studies from R3 and found at Waregi Hill suggest the occurrence of a closed-canopy forest environment during the deposition of the upper Kibanga Member. Paleontological studies of faunal occurrence and abundance data from the R1 and R3 fossil sites confirm significant differences in the fossil communities, interpreted to be the result of these habitat differences over time. Taken together, these results suggest that some previous paleoecological reconstructions of the Hiwegi may have suffered from time-averaging or sampling different time intervals under the assumption they were correlative. Despite basic differences between faunas demonstrated here, additional systematic excavations need to be done at Rusinga Island and at other sites across East Africa to determine how fauna responded to environmental changes in the early Miocene.

These results from Rusinga Island offer an important contrast to the historical argument that the early Miocene of Africa was characterized by a “Pan-African” forest. Other sites have documented both open and closed conditions during the late Oligocene and early Miocene, which likely strongly influenced the evolution of vegetation and mammalian communities. The presence of early apes within a variety of closed and open environments calls into question the role of forested habitats in differentiating basal hominoids.

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Figure Captions

Figure 1. (A) and (B) Generalized geologic map of Rusinga Island, Kenya in Lake Victoria. Major fossil localities are indicated by their site number designation (adapted from Van Couvering, 1972). Waregi Hill and fossil sites R1, R1A, and R3 are the focus of this study. (C) Generalized stratigraphy for early Miocene rocks on Rusinga Island. Stratigraphic position of Hiwegi Formation indicated by gray box. Fm = Formation and Mbr = Member.

Figure 2. Lithostratigraphic section from Waregi Hill. Note break in scale in Kiangata Formation. Stratigraphic position of paleosols (labelled P1-P11) and the ‘marker bed’ used for correlation across Waregi Hill are indicated by arrows. The fossiliferous units that comprise the R1 fossil locality occur between ~21 and 32 m in the lithostratigraphic section, with the top and bottom of the interval indicated by bone drawings. Strata correlative to the R3 fossil locality occur between ~45 and 55 m and are labeled as “R3 interval”.

Figure 3. Photographs of observations made in the field. (A) Pedogenic carbonate seen in P1 of the Waregi Member of the Hiwegi Formation at R1. (B) Siltstones with satin-spar calcite pseudomorphous after gypsum deposits from the lower Waregi Formation at Waregi Hill. There are two layers pointed out here, the upper one is laterally correlative across R1. (C) Calcified root traces from the upper Waregi Formation. (D) Volcaniclastic deposits of the Kibanga Member. (E) Carbonate nodules seen in cross-section in a paleosol from the Kibanga Member.

Figure 4. Photomicrographs from upper siltstone marker bed at R1. All images are under Plane-Polarized Light (PPL) unless otherwise noted. (A) Sparry calcite displacing siltstone matrix. (B) Sparry calcite cement and illuviated clay and b-fabric. (C) Sparry calcite, and Fe-Mn oxide dendritic growth in matrix. (D) Close up (red box in C) showing sparry calcite cement and infilling of secondary porosity. Clastic grains have clay rings and there is B-fabric seen in the matrix (10x). (E) B-fabric in siltstone matrix. (F) Sparry calcite and illuviated clay around sericitized field spar grains.

Figure 5. Photomicrographs from paleosols and other sedimentary rocks from the upper Hiwegi Formation (Grit/Fossil Bed Member and Kibanga Member). All images are under PPL unless noted. (A) Basalt clast with Fe-Mn oxide weathering rind from the Grit/Fossil Bed Member. (B) Basalt cobbles with weathering rind from the Grit/Fossil Bed Member. (C) Pedogenic, micritic calcite nodule with Fe-Mn oxide rind. (D) Pedogenic carbonate nodule (black circle) from the Hiwegi Formation. (E) Fe-Mn oxide dendritic growths (black arrows) and weathered pyroxenes in paleosol matrix from Hiwegi Formation in PPL light and (F) Cross-Polarized Light (XPL). (G) Volcanic glass (black arrow) in siliclastic matrix. (H) Sparry calcite cement rimming feldspar grains under XPL conditions.

Figure 6. Photomicrographs from paleosols and other sedimentary rocks from the upper Hiwegi

Formation (Grit/Waregi Member and Kibanga Member). All images are under PPL unless noted. (A) Calcite nodule in paleosol matrix. (B) Lapilli fragments in various stages of weathering. (C) Weathered clay rind (black arrow) along lapilli fragment from the P10 at R3. (D) Burrow structure (possibly sweat bees) from P10 at R3. (E) Sparry calcite infilling a termite termitaria structure from P10 at R3. (F) Fossilized oribatid mite fecal material (white arrows) inside a root cast (black arrows) from the P10 paleosol at R3. This image was taken under 100x magnification. (G) Illuviated clay from the P10 paleosol at R3.

Table 1. Mammalian faunal list (at the genus level) for the R1 and R3 sites (Hiwegi Fm.) on Rusinga Island (including REACHE surveys). The faunal list by Pickford (1986) has been taxonomically and systematically updated.

Table 2. Comparison of the taxonomic composition (at the genus level) of the mammalian fauna found in R1 and R3 sites (Hiwegi Formation) on Rusinga Island. Jaccard similarity coefficient and Sørensen–Dice index (see Lyman, 2008) are calculated on the basis of the faunal lists given in Table 1. Taxa above the genus level are excluded.

Table 3. Composition of the mammal fauna from R1 and R3 (Hiwegi Fm.) on Rusinga Island, based on the REACHE collections (2006 to 2016).

GROUP	FORMATION	C	
Kisingiri	Lunene Lavas		
	Kiangata Agglomerate		
Rusinga	Kulu Fm.		
	Hiwegi Fm.	Kibanga Mbr.	
		Fossil Bed Mbr/Grit Mbr.	
		Kaswanga Point Mbr	
	100	Rusinga Agglomerate	
		Kiahera Fm.	
	0 m	Wayondo Fm.

(A)

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(C)

(D)

(E)

(F)

Sedimentology

Taxon	R1			R2	
	after Pickford (1986)	This Project		after Pickford (1986)	2008-16 (ALL)
		2006-16 (ALL)	"Rodent Hill"		
Primates	x	x	x	x	x
<i>Dendropithecus</i>	x	x		x	x
<i>Ekembo</i>	x	x	x	x	x
<i>Komba</i>	x			x	
<i>Limnopithecus</i>	x	x		x	x
<i>Mioeuoticus</i>	x			x	
<i>Nyanzapithecus</i>	x	x		x	
<i>Propotto</i>				x	
Chiroptera				x	
Lagomorpha	x	x	x	x	x
<i>Kenyalagomys</i>	x	x	x	x	x
Rodentia	x	x	x	x	x
<i>Diamantomys</i>	x	x	x	x	x
<i>Epiphiomys</i>		x	x		
<i>Kenyamys</i>		x	x		x
<i>Lavocatomys</i>		x	x		x
<i>Megapedetes</i>	x	x		x	x
<i>Nonanomalurus</i>					x
<i>Notocricetodon</i>		x			
<i>Paranomalurus</i>		x			x
<i>Paraphiomys</i>	x	x	x	x	x
<i>Proheliophobius</i>	x	?	?		
<i>Protarsomys</i>		x			
<i>Rusingapedetes</i>		x			
<i>Simonimys</i>		x	x		x
<i>Vulcanisciurus</i>	x	x	x	x	x
Macroscelidea	x	x	x	x	?
<i>Miorhynchocyon</i>		x	x		
<i>Myohyrax</i>	x	x		x	
Tenrecidae	x	x		x	
<i>Parageogale</i>				x	
<i>Protenrec</i>	x				
Proboscidea	x	x	x	x	x
Gomphotheriidae ¹	x			x	x
<i>Prodeinotherium</i>	x	x		x	x
Hyracoidea	x	x		x	x
<i>Afrohyrax</i>	x	x		x	x
<i>Meroehyrax</i>	x				
Tubulidentata	x	x		x	x
<i>Myorycteropus</i>	x	x		x	x
Ptolemaiida		?			
<i>Kelba</i>		?			
Erinaceidae	x	x	x	x	x

<i>Amphechinus</i>	x	x	x	x	x
<i>Galerix</i>		x	x		
<i>Gymnurechinus</i>	x	x	x	x	
Hyaenodontidae	x	x		x	?
<i>Anasinopa</i>	x	x		x	
<i>Hyainailouros</i>				x	
<i>Isohyaenodon</i>	x			x	
<i>Leakitherium</i>				x	
<i>Metapterodon</i>				x	
Carnivora	x	x	x	x	x
<i>Afrosmilus</i>		x			x
<i>Cynelos</i>	x			x	
<i>Herpestides</i>		x			
<i>Kichechia</i>	x	x	x	x	
<i>Luogale</i>		x	x		
Rhinocerotidae	x	x		x	x
<i>Brachypotherium</i>	x				
<i>Rusingaceros</i>	x				
<i>Turkanatherium</i>	x			x	
Chalicotheriidae	x	x		x	x
<i>Butleria</i>	x	x		x	x
Anthracotheriidae	x	x		x	?
<i>Brachyodus</i>	x	x		x	?
<i>Sivameryx</i>	x			x	
Suidae	x	x		x	x
<i>Kenyasus</i>	x	x		x	x
<i>Kubanochoerus</i>	x	x		x	
<i>Nguruwe</i>	x	x		x	
Sanitheriidae	x	x		x	x
<i>Diamantohyus</i>	x	x		x	x
Ruminantia	x	x	x	x	x
<i>Canthumeryx</i>		x		x	
<i>Dorcatherium</i>	x	x	x	x	x
<i>Propalaeoryx</i>	x	x		x	
<i>Walangania</i>	x	x		x	

¹*Gomphotheriidae* sp. is indicated here for discussion purposes

? = Tentative identification.

3	
This Project	
Forest paleosol	Ravine
x	x
x	
x	
	x
x	x
x	x
x	x
x	x
x	
x	
x	x
x	
x	x
x	
?	
x	x
x	
	x
x	
x	
x	?
x	
x	

x

?

x

x

x

x

x

x

?

?

x

x

x

x

x

x

x

x

x

Taxon	R1			
	ALL		"Rodent Hill"	
	NISP	%	NISP	%
Primates				
<i>Dendropithecus</i>	4	1.00%		
<i>Ekembo</i>	7	1.70%	1	1.10%
<i>Limnopithecus</i>	1	0.20%		
<i>Nyanzapithecus</i>	1	0.20%		
Lagomorpha				
<i>Kenyalagomys</i>	29	7.20%	5	5.70%
Rodentia				
<i>Diamantomys</i>	11	2.70%	2	2.30%
<i>Epiphomys</i>	2	0.50%	1	1.10%
<i>Kenyamys</i>	2	0.50%	2	2.30%
<i>Lavocatomys</i>	7	1.70%	1	1.10%
<i>Megapedetes</i>	3	0.70%		
<i>Nonanomalurus</i>				
<i>Notocricetodon</i>	1	0.20%		
<i>Paranomalurus</i>	1	0.20%		
<i>Paraphiomys</i>	106	26.30%	25	28.70%
<i>Proheliophobius</i>	1	0.20%	1	1.10%
<i>Protarsomys</i>	1	0.20%		
<i>Rusingapedetes</i>	1	0.20%		
<i>Simonimys</i>				
<i>Vulcanisciurus</i>	2	0.50%	1	1.10%
Macroscelidae				
<i>Myohyrax</i>	3	0.70%		
<i>Miorhynchocyon</i>	1	0.20%	1	1.10%
Proboscidea				
<i>Prodeinotherium</i>	3	0.70%		
Gomphotheriidae sp.	1	0.20%		
Hyracoidea				
<i>Afrohyrax</i>	46	11.40%		
Tubulidentata				
<i>Myorycteropus</i>	9	2.20%		
Ptolemaiida				
<i>Kelba</i>	1	0.20%		
Erinaceidae				
<i>Amphechinus</i>	2	0.50%	1	1.10%
<i>Galerix</i>	2	0.50%	2	2.30%
<i>Gymnurechinus</i>	2	0.50%	1	1.10%
Hyaenodontidae				
<i>Anasinopa</i>	1	0.20%		
Carnivora				
<i>Afrosmilus</i>				
<i>Kichechia</i>	1	0.20%		

<i>Luogale</i>	1	0.20%	1	1.10%
Chalicotheriidae				
<i>Butleria</i>	5	1.20%		
Anthracotheriidae				
<i>Brachyodus</i>	4	1.00%		
Suidae				
<i>Kenyasus</i>	4	1.00%		
<i>Kubanochoerus</i>	3	0.70%		
Sanitheriidae				
<i>Diamantohyus</i>				
Ruminantia				
<i>Canthumeryx</i>	3	0.70%		
<i>Dorcatherium</i>	123	30.50%	42	48.30%
<i>Propalaeoryx</i>	3	0.70%		
<i>Walangania</i>	5	1.20%		
Total NISP	403		87	

All specimens identified to genus level are included. R1 ALL includes the sub-set R1 "Rodent Hill." R3 ALL include stratigraphic provenance. For each collection, the most abundant taxa are in boldface. NISP = Number of Indi

R3					
ALL		Forest Paleosol		Ravine	
NISP	%	NISP	%	NISP	%
1	0.50%	1	0.90%		
2	1.00%	2	1.80%		
1	0.50%			1	4.80%
14	7.30%	3	2.70%	2	9.50%
25	13.00%	17	15.50%	2	9.50%
1	0.50%	1	0.90%		
3	1.60%	2	1.80%		
3	1.60%	1	0.90%	2	9.50%
1	0.50%	1	0.90%		
75	38.90%	45	40.90%	8	38.10%
1	0.50%				
2	1.00%	1	0.90%		
4	2.10%			1	4.80%
3	1.60%	3	2.70%		
14	7.30%	7	6.40%		
6	3.10%	2	1.80%	2	9.50%
1	0.50%	1	0.90%		
1	0.50%	1	0.90%		

1	0.50%	1	0.90%		
1	0.50%	1	0.90%		
1	0.50%	1	0.90%		
2	1.00%	1	0.90%		
1	0.50%	1	0.90%		
30	15.50%	18	16.40%	3	14.30%
<hr/>					
193		110		21	
<hr/>					

as specimens found in the ravine and forest paleosol exposures, but also specimens without clear individual Specimen; % refers to relative abundance.

	R1 ALL	R1 “Rodent Hill”	R3 ALL	R3 Ravine	R3 Forest paleosol
R1 ALL		0.57	0.54	0.33	0.54
R1 “Rodent Hill”	0.4		0.53	0.33	0.51
R3 ALL	0.37	0.36		0.53	0.93
R3 Ravine	0.2	0.2	0.37		0.52
R3 Forest paleosol	0.39	0.35	0.86	0.35	

Jaccard similarity coefficient

Sørensen–Dice index