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Lake Victoria, Kenya

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Abstract

The Early Miocene of Rusinga Island (Lake Victoria, Kenya) is best known for its vertebrate fossil assemblage—particularly of early hominoids and catarrhines—but the multiple stratigraphic intervals with well-preserved fossil leaves have received much less attention. The Hiwegi Formation has three fossil leaf-rich intervals: Kiahera Hill, R5, and R3. Here, we made new fossil collections from Kiahera Hill and R3 and compared these floras to previous work from R5 as well as modern African floras. The Kiahera Hill flora was most similar to a modern tropical rainforest or tropical seasonal forest and was a warm and wet, closed forest. This was followed by a relatively dry and open environment at R5, and R3, which was most similar to a modern tropical seasonal forest, was a warm and wet spatially heterogenous forest. Floral composition of these floras differed dramatically but Kiahera Hill and R3 were more similar to each other than either flora was to R5. The Kiahera Hill flora had few monocots or herbaceous taxa and was dominated by large leaves and had a higher species richness and greater evenness than the R3 flora. Our work, coupled with previous studies, suggests that R3 had a landscape of

both closed forest and more open areas with seasonal ponding. The absence of morphotypes from the R5 flora that were present in the Kiahira Hill and R3 floras provides evidence for local expatriation during the R5 time interval. These results demonstrate that there was a considerable change in both climate and vegetation over an ~500 kyr interval of the Kiahira Hill, R5, and R3 floras. Thus, this work suggests that the Hiwegi Formation on Rusinga Island samples multiple environments in the Early Miocene and provides important context for the evolution and habitat preference of early apes.

Keywords: paleobotany; paleoclimate; leaf physiognomy; hominids

I. Introduction

Rusinga Island is located in Lake Victoria, western Kenya within the Nyanza Rift on the margin of the extinct Kisingiri volcano (Figure 1). Early Miocene fossils from Rusinga Island provide critical context for the evolution of early hominoids. Previous fieldwork has uncovered more than 100 mammal species, as well as numerous other vertebrate, invertebrate and plant fossils (e.g., Chesters 1957; Pickford 1986; Drake et al. 1988; Peppe et al. 2009; Maxbauer et al. 2013; Michel et al. 2014, in press; Čerňanský et al. 2020). In particular, the Miocene deposits on Rusinga Island are best known for the occurrence of numerous, well-preserved fossil primates, such as the stem catarrhine *Ekembo* (e.g., MacInnes 1943; Le Gros Clark and Leakey 1951; Andrews and Simons 1977; Walker and Teaford 1988; Walker et al. 1993; McNulty et al. 2015).

Figure 1. Adapted from Maxbauer et al. (2013). (1) A map showing Africa, star indicates approximate location of Lake Victoria, Rusinga Island and Mfangano Island. (2) Generalized map of Rusinga Island including basic stratigraphic distributions and general site locations. Stars indicate the approximate location of study's locations (1 = Kiahera Hill, 2 = R5, 3 = R3). (3) Generalized Miocene stratigraphy on Rusinga Island. Stars indicates stratigraphic position of fossil leaf localities. Mbr. = member, Fm. = formation.

In order to interpret the abundant and diverse vertebrate fossil assemblages on Rusinga Island, we must first answer the following question: what was the paleoenvironment and paleoclimate of the region during the Early Miocene? Previous researchers have tried to answer this question using faunal analysis, paleobotany, stable isotope geochemistry, and quantitative and qualitative analyses of paleosols, but reconstructions have been contradictory and have ranged from tropical rainforests to semi-arid environments (Chesters 1957; Andrews and Van

Coupling 1975; Evans et al. 1981; Collinson 1985; Retallack et al. 1995; Andrews et al. 1997; Bestland and Krull 1999; Collinson et al. 2009; Maxbauer et al. 2013; Michel et al. 2014, in press). However, most reconstructions have indicated open woodland or closed canopy forest environments (e.g., Andrews and Van Coupling 1975; Evans et al. 1981; Collinson 1985; Retallack et al. 1995; Collinson et al. 2009; Maxbauer et al. 2013; Michel et al. 2014). The vegetation density and structure of a woodland versus a closed-canopy forest are dramatically different and would cause distinct selective and environmental pressures on mammal communities. Thus, an accurate reconstruction of the paleoenvironment and paleoclimate of Rusinga Island in the Early Miocene is vital for interpreting its mammalian assemblages.

Systematic analyses of fossil leaves provide a unique perspective of the environments present on Rusinga Island in the Early Miocene and can help solve the conundrum of the contradictory reconstructions for two important reasons. First, the size and shape (physiognomy) of non-monocotyledonous angiosperm leaves are indicators of paleoclimate and paleoenvironment (e.g., Jacobs 2004; Peppe et al. 2011, 2018). For example, the proportion of woody dicotyledonous angiosperm (woody dicots) species with entire margins at a site increases with higher mean annual temperature (MAT) and variables related to tooth count and size negatively correlate with MAT, while the average leaf size of woody dicots in a flora increases with higher mean annual precipitation (MAP) (e.g., Bailey and Sinnott 1915, 1916; Jacobs 1999, 2002, 2004; Peppe et al. 2011, 2018; Schmerler et al. 2012). Second, leaves cannot be transported intact over great distances and therefore represent the local environment (e.g., Burnham et al., 1992; Burnham 1994; Greenwood 2007; Ellis and Johnson 2013; Peppe et al. 2018). Thus, analyses of the abundant fossil leaves on Rusinga Island can directly reconstruct the

local paleoclimate during the Early Miocene. Furthermore, quantitative assessments of the floral community composition and diversity can also help better constrain ecosystem structure and how it may have changed through time, which provides critical information for understanding the life history and evolutionary pressures on the Early Miocene vertebrate fauna.

However, despite their considerable potential as paleoenvironmental indicators and that plant fossils have been documented throughout the Rusinga stratigraphy for over one hundred years (e.g., Muff 1908; Chesters 1957; Van Couvering, 1972; Collinson 1985; Pickford 1986), plant fossils have received much less attention than the fossil vertebrate fauna. Early research on fossil leaves was primarily focused on taxonomic identifications, qualitative environmental reconstructions, and the documentation of the occurrence of fossil plants in the stratigraphy (e.g., Muff 1908; Chesters 1957; Van Couvering 1972; Pickford 1986). Furthermore, despite being abundant and commonly found, analyses of leaf fossils have primarily only incorporated them anecdotally or were based on very small sample sizes, poorly preserved specimens and/or samples with poor locality and stratigraphic resolution (e.g., Chesters 1957; Retallack et al. 1995; Collinson et al. 2009). More recently, work has focused on making systematic collections of fossil plants and utilizing modern analytical techniques to identify taxa (Collinson et al. 2009; Maxbauer et al. 2013; Michel et al. 2014; Adams et al. 2016). Of these studies, only two specifically focused on collecting and analyzing fossil leaves for paleoenvironmental reconstructions (Maxbauer et al. 2013; Michel et al. 2014). However, neither of these studies made systematic census collections making it impossible to reconstruct floral abundance and diversity of the floras.

Here we present the first comprehensive paleobotanical paleoclimate and paleoenvironment reconstructions from the Early Miocene from multiple intervals in the Hiwegi Formation of Rusinga Island based on systematic census collections from two sites near the base and the top of the Hiwegi Formation: Kiahera Hill and R3 (Figure 1). We also assessed fossil leaves that were previously collected from the R3, R5, and Kiahera Hill localities that are housed at the National Museums of Kenya (NMK) (Figure 1, Table 1), and compared our new results to previous paleobotanical studies from R5 and R3 (Maxbauer et al. 2013; Michel et al. 2014). These data, coupled with regional paleoenvironmental reconstructions, were then used to provide vital context for early hominoid evolution in East Africa in the Early Miocene.

2. Geologic Setting and Paleoenvironmental Reconstructions

Modern Rusinga Island is located in western Kenya in Lake Victoria (Figure 1). During the Miocene, Rusinga and Mfangano Islands were located at the outer margin of the crustal depression of the large carbonatite-nephelinite Kisingiri volcano, at the mouth of the Winan (formerly Kavirondo) Gulf in the failed Nyanza Rift and predates the formation of Lake Victoria (Van Couvering 1972; Drake et al. 1988; Bestland 1991). The stratigraphic nomenclature used here follows Michel et al., (in press), Peppe et al. (2009), and Van Couvering (1972) (Figure 1). Exposures on Rusinga Island encompass the Rusinga Group and the Kisingiri Group; the Rusinga Group consists of the volcanoclastic and tuffaceous Wayando Formation, Kiahera Formation, the Rusinga Agglomerate, Hiwegi Formation, and the primarily non-volcanic Kulu Formation. The Hiwegi Formation is composed of the Kaswanga Point, Grit/Fossil Bed, and Kibanga Members (Michel et al. in press; Van Couvering 1972; Drake et al. 1988; Peppe et al. 2009). Previously, K-Ar dates published by Drake et al. (1988) suggested that the Hiwegi

Formation was deposited at ~17.9 Ma and that the entire Rusinga Group sequence was deposited in less than 500 kyr. However, more recent work using $^{40}\text{Ar}/^{39}\text{Ar}$ dates, magnetostratigraphy, and lithostratigraphy demonstrate that the Rusinga Group was deposited over a longer time interval, between ~17-20 Ma, and that the deposition of the fossil-rich Hiwegi Formation spans more than 100 kyr (Peppe et al. 2009, 2011, 2016, 2017; McCollum et al. 2012).

Sub-locality	Site	GPS coordinates	Census or voucher	No. identifiable leaves	No. morphotypes
DP1124	Kiahera Hill		Voucher	52	11
RU2012	Kiahera Hill		Voucher	110	14
AB1801	Kiahera Hill	S 00° 25.000' E 34° 09.320'	Voucher	41	15
AB1801C	Kiahera Hill	S 00° 25.009' E 34° 09.319'	Census	317	15
AB1801A	Kiahera Hill	S 00° 24.998' E 34° 09.321'	Census	318	18
	<i>Kiahera Hill total</i>			838 (635)	40 (34)
DP1111	R3		Voucher	92	20
RU2012	R3		Voucher	16	14
AB1802	R3	S 00° 24.005' E 34° 12.885'	Both	405	15
AB1803	R3	S 00° 23.985' E 34° 12.897'	Census	692	21
AB1804	R3	S 00° 24.003' E 34° 12.872'	Voucher	5	3
AB1805	R3	S 00° 24.017' E 34° 12.872'	Voucher	10	6
AB1806	R3	S 00° 24.035' E 34° 12.880'	Census	228	13
AB1806A	R3	S 00° 24.026' E 34° 12.883'	Census	56	8
	<i>R3 total</i>			1504 (1396)	52 (39)

Table 1. Sampling summary of Kiahera Hill and R3. Numbers in parentheses only include collections by AB.

2.1 Previous Work

Previous paleoenvironmental reconstructions of the Hiwegi Formation using a variety of methods including faunal analysis, paleobotany, geochemistry, and quantitative and qualitative analyses of paleosols, have ranged from a tropical rainforest to a semi-arid environments (e.g., Chesters 1957; Andrews and Van Couvering 1975; Evans et al. 1981; Collinson 1985; Thackray 1994; Retallack et al. 1995; Bestland and Krull 1999; Forbes et al. 2004; Collinson et al. 2009; Ungar et al. 2012; Maxbauer et al. 2013; Michel et al. 2014). The reason for these contradictory results is likely in large part due to sampling resolution and methodology. Previous work that examined data from the entire Hiwegi Formation (e.g., Andrews and Van Couvering 1975; Evans et al. 1981; Retallack et al. 1995; Forbes et al. 2004; Ungar et al. 2012) likely sampled a mixture of environments from different time periods, which resulted in an imprecise “time-averaged” environmental reconstruction. Conversely, other research focused on a limited stratigraphic interval (e.g., Collinson 1985; Thackray 1994; Collinson et al. 2009; Maxbauer et al. 2013; Michel et al. 2014) likely represents a restricted interval of time. Relatively few studies have attempted to reconstruct paleoenvironment through time. Recently, Michel et al. (in press) conducted detailed sedimentological analyses through the Hiwegi Formation and demonstrated that environments changed through the formation, ranging from drier, more open environments to wetter, closed canopy forests. Further, their results provide evidence for habitat heterogeneity spatially and temporally in the Hiwegi Formation. Thus, the discrepancy in sampling in previous paleoenvironmental research (i.e., stratigraphically restricted versus time-averaged) likely contributes to the range of paleoenvironmental interpretations in the literature.

Few studies have focused on the paleobotany of Early Miocene Rusinga Island. Initial work by Chesters (1957) examined fossil woods and seeds from Rusinga and Mfangano Islands,

which indicated a tropical rainforest or gallery forest regional paleoenvironment. However, this conclusion was based on fossil material from surface collections from multiple sites of different ages and therefore is likely an unreliable paleoenvironmental reconstruction due to time-averaging. Nearest living relative (NLR) analyses of the R117 site in the Grit/Fossil Bed Member by Collinson (1985) and Collinson et al. (2009) used *in situ* fruits (including from a monocotyledonous palm), seeds, and wood of dicotyledonous angiosperms trees, herbaceous climbers, and lianas, and concluded that the local paleoenvironment was a woodland with little nearby forest based on the determination that the flora consisted of only 4.2% definitively forest dwelling taxa (for a complete taxon list see Collinson et al. 2009). Similarly, work on the R5 site in the Grit/Fossil Bed Member by Maxbauer et al. (2013), which samples a similar stratigraphic interval to the study of Collinson et al. (2009), determined that the local paleoenvironment was a riparian habitat with a patchwork woodland and forest within a warm local climate based on fossil floral and sedimentological evidence. Finally, work on the R3 site in the Kibanga Member by Michel et al. (2014) based on paleopedology and paleobotany determined that the local paleoenvironment was a widespread, dense, multistoried, closed-canopy tropical seasonal forest in a warm and relatively wet local climate. Unlike Chesters (1957), the reconstructions by Collinson (1985), Collinson et al. (2009), Maxbauer et al. (2013), and Michel et al. (2014) likely reflect the local paleoenvironment during a relatively short interval of time due to their stratigraphic restriction and quantitative sampling strategy.

As noted above, when taken in total, previous reconstructions demonstrate that the local paleoenvironment varied throughout the deposition of the Hiwegi Formation, changing from a mosaic forest or woodland in the Grit/Fossil Bed Member to a dense closed-canopy forest in the

Kibanga Member (Collinson et al. 2009; Maxbauer et al. 2013; Michel et al. 2014, in press; Peppe et al. 2016). These differences between open woodland and closed forest have significant implications for the evolution of early catarrhine primates because woodlands and forests have different density and structure of vegetation, which determines the inhabiting species (Reed and Bidner 2004). In particular, woodland environments are composed of smaller trees with minimal canopy overlap, while tropical forests are composed of large trees (20 m or taller) with a fully closed canopy (Jacobs 2004). Therefore, understanding the extent of the differences in vegetation structure and how it changed through time is important for interpreting the Miocene fauna of Rusinga Island. In order to corroborate the results of previous paleobotanical and paleoenvironmental studies, large collections of fossil leaves are required, particularly from additional stratigraphic intervals to assess how rapidly paleoclimate, paleoenvironment, and plant communities changed through time, which is the focus of this study.

2.2 Study Area

Fossil plant material for this study was systematically collected from two sites within the Hiwegi Formation: Kiahera Hill and R3 (Figure 1, Table 1). These new census collections were used to supplement existing voucher collections from R5 (Maxbauer et al. 2013), R3 (Michel et al. 2014), and Kiahera Hill housed at the NMK.

The Kiahera Hill site is the oldest site in this analysis and is located at the base of the Hiwegi Formation in the Kaswanga Point Member (Figure 1). The Kiahera Hill site is within a relatively thin (<0.5 m thick) stratigraphic unit that is exposed around the perimeter of Kiahera Hill. Fossil leaves were located in a mudstone lens underlying a tuffaceous ash layer. The leaf

layer was often preserved as mat of leaf litter, and therefore it could be difficult to differentiate individual leaves.

The R5 site is located near the middle of the Hiwegi Formation in the Grit/Fossil Member (Figure 1) (Maxbauer et al. 2013). Fossil leaves at R5 were collected from very fine grain sandstone layer with ripples. Many of the leaves were fragmentary and conforming to ripples. The fragmentary nature of the fossil leaves, as well as their preservation on rippled bedforms, suggests that the leaves may have been transported a short distance before deposition. The small sample size and fragmentary nature of the fossil leaves meant that analyses were primarily qualitative. For a complete overview of the R5 flora, see Maxbauer et al. (2013).

The R3 site is from near the top of the Kibanga Member of the Hiwegi Formation (Figure 1) and is a rich vertebrate fossil locality with abundant paleosols and preserved stump casts (Michel et al. 2014). The fossil flora was previously published by Michel et al. (2014), but the work was based on a relatively small voucher collection and only preliminary morphotype identifications were assigned to the flora. In this study and in Michel et al. (2014), fossil leaves were collected from a series of thin mudstone lenses at the base of the coarse-grained sandstone overlying the forested paleosol horizon and were stratigraphically correlated across the site. Leaf preservation was primarily solitary, and leaves were often preserved in coarse grained “mud balls”. Vertebrate fossils are not preserved in the fossil leaf layers, but a few gastropod shells were recovered.

3. Methods

3.1 Collections

Plant fossils were collected from five localities at the R₃ site and two localities at the Kiahera Hill site. Fossils collected as vouchers were selected based on preservation. Census collections were made in July 2018. Localities were assigned a code based on the initials of the researcher, the year, and the order the site was found. For example, AB1804 was the fourth site found by Aly Baumgartner in 2018. In addition, voucher collections from Kiahera Hill and R₃ were made in 2011 and 2012 and were included in analyses (Table 1).

Census collections were made following established protocols (e.g., Johnson 2002; Wilf and Johnson 2004; Peppe 2010). For census collections, all specimens were assigned to morphotypes in the field, and the number of specimens per morphotype were tallied. A morphotype is a morphologically distinct group of specimens and while morphotypes have no formal taxonomic assignment, they often reflect biological species (see reviews of morphotyping method in Ash 1999; Peppe et al. 2008; and Ellis et al. 2009). During census collections, a representative sample of the field morphotypes, as well as an unidentified specimens and additional exceptionally preserved fossils were collected. At least 300 identifiable specimens were tallied for census collections because modern taphonomic studies of forest leaf litter have indicated that at least 300 specimens are required to accurately reflect forest composition (e.g., Burnham 1989; Burnham et al. 1992, 2001). Fossil leaves were collected using the bench and quarry method by removing large blocks of rock to be split along bedding planes to expose leaf-bearing horizons (see Johnson et al. 1989). Because the fossiliferous layers were relatively thin (~5-20 cm thick), each fossil quarry covered a few square meters. The lithology and sedimentary

features of each locality were recorded to determine their specific depositional environments. All specimens are curated at the NMK.

At Kiahera Hill the leaf-bearing layer is exposed around the perimeter of the hilltop, therefore the voucher collection AB1801 consists of fossils collected around the perimeter of the hill rather than from a single quarry. Two census collections were made from one site at Kiahera Hill (AB1801C and AB1801A) (Table 1).

At R₃, voucher collections were made at AB1802, AB1804, and AB1805. Census collections from R₃ were made at AB1802, AB1803, AB1806, and AB1806A along a 100 m transect to test for lateral heterogeneity. Because census collections are based on identifiable specimens and the census collections from R₃ were artificially dominated by monocot morphotypes due to their ease of identification (i.e., larger leaf fragments were required to identify dicot morphotypes than monocot morphotypes), an “indeterminate dicot” morphotype was included in order to calculate a more accurate proportion of monocots to dicots.

At the NMK, all identifiable fossil leaves were assigned Hiwegi Formation morphotypes. These morphotypes were denoted by the prefix HW and assigned a number (e.g. HW-12). Morphotypes were described following the well-established protocols of the *Manual of Leaf Architecture* (Ellis et al. 2009) (Supplementary Material).

3.2 Paleoclimate

All samples were photographed for paleoenvironment and paleoclimate estimates. Photographs of all fossil leaves were taken using a high-resolution camera (Canon Eos Rebel T6, DX-VR, 18-55 mm). All photographs include a scale bar and field number. Leaves were digitally removed from the rock matrix and prepared in Adobe Photoshop 8.0 (Adobe Systems Inc., San Jose, California, USA) and digital measurements were made using ImageJ (Abràmoff et al. 2004) .

The mean annual temperature (MAT) and mean annual precipitation (MAP) were estimated using univariate and multivariate leaf physiognomic paleoclimate proxy methods. The univariate methods leaf margin analysis (LMA) (Wilf 1997; Peppe et al. 2011, 2018) and leaf area analysis (LAA) (Wilf et al. 1998; Jacobs 2002; Peppe et al. 2018) were used to estimate MAT and MAP, respectively. All well preserved, non-aquatic, woody dicot angiosperm leaves were also measured using the Digital Leaf Physiognomy (DiLP) protocol (Huff et al. 2003; Royer et al. 2005; Peppe et al. 2011). For DiLP analyses, margin state was the only character recorded for leaves that were not sufficiently well-preserved to measure the other characters. For specimens that were sufficiently well-preserved, leaf size was reconstructed in order to measure inferred blade area, inferred major axis length, and inferred Feret diameter. Toothed leaves were measured if at least 25% of the leaf area and margin was preserved with at least two consecutive teeth. For toothed specimens that were sufficiently well-preserved, the damaged margin was digitally removed, and the total number of teeth, undamaged perimeter length, and undamaged leaf area were measured. See Royer et al. (2005) and Peppe et al. (2011) for a complete description of leaf characters used in DiLP, and Peppe et al. (2011) for a detailed protocol for processing fossil leaves.

For leaves that were not sufficiently well-preserved to reconstruct leaf area using a direct measurement, leaf area was estimated using the vein scaling method (Sack et al. 2012; Merkhofer et al. 2015). Secondary veins (2°) were identified using the definition of Ellis et al. (2009) and included all regular, inter-, interior, and minor secondaries. Four rectangular boxes were digitally placed on partial fossil leaves using Adobe Photoshop 8.0. When possible, boxes were located on the basal, middle and apical thirds of the leaf—two boxes were placed in the middle third, one near the primary vein and one near the margin—following the methods of Sack et al., (2012) and Merkhofer et al., (2015). If that was not possible, the boxes were fit on the available preserved area. For lobed leaves, each lobe was measured separately and the values were combined. The area of each rectangle was sized to include at least two 2° veins. After measuring and recording the area of each box, the lengths of all secondary veins were measured and recorded. Vein density was defined as the total vein length divided by the area of the rectangle following Sack et al. (2012). All measurements were made in ImageJ. After calculating the average vein length density (mm/mm^2) for all specimens, the estimated area of each leaf was scaled using the regression method of Sack et al. (2012). The estimated leaf area was recorded in mm^2 and the natural log of the estimated leaf area was used to categorize each leaf into the following leaf sizes: leptophyll, nanophyll, microphyll, notophyll, mesophyll, and megaphyll. These categories were defined as greater than 2.12 mm^2 , 4.32 mm^2 , 6.51 mm^2 , 8.01 mm^2 , 9.11 mm^2 , and 11.42 mm^2 , respectively (Webb 1959).

3.3 Paleoenvironment

Leaf mass per area (M_A) correlates strongly with leaf lifespan (i.e., if a leaf is evergreen or deciduous) (Wright et al. 2004; Royer et al. 2012). Leaves with high M_A tend to be thicker and

evergreen, while leaves with low M_A tend to be thinner and deciduous (Wright et al. 2004). M_A was estimated using the scaling relationship between leaf area, petiole width—or when the petiole was missing the primary vein width at the base of the leaf—and M_A (Royer et al. 2007, 2010; Peppe et al. 2014). Following the methods of Royer et al. (2007), fossil leaves with $< \sim 87 \text{ g m}^{-2} M_A$ were categorized as deciduous, $\sim 111 \text{ g m}^{-2} M_A$ were categorized as semi-deciduous and $> \sim 129 \text{ g m}^{-2} M_A$ were categorized as evergreen.

3.4 Statistical Analyses

All analyses of floral diversity were performed in *R* version 3.6.2 (R Development Core Team, Vienna, Austria). Methods were based on Currano et al. (2011). We analyzed species richness and evenness for the Kiahera Hill and R3 sites, as well as heterogeneity for R3. Floral richness was measured using analytical rarefaction to standardize species for sample size (“iNEXT”, Chao et al. 2014; Hsieh et al. 2020). Simpson’s index of diversity was calculated for Kiahera Hill and R3 (“vegan”, Oksanen et al. 2019). Probability of interspecific encounter (PIE) was used to compare evenness among sub-localities and between Kiahera Hill and R3 (“benthos”, Walvoort 2019). For R3, floral heterogeneity was quantified by calculating the Jaccard dissimilarity between all pairs of sub-localities (“vegan”, Oksanen et al. 2019). Dissimilarity was calculated from a matrix of plant species presence or absence. The results were averaged within each locality to obtain a single value for heterogeneity.

4. Results

4.1 Kiahera Hill Paleoenvironment, Paleoecology and Paleoclimate

Forty morphotypes were identified from more than 800 leaves collected from Kiahera Hill (Table 1). The Kiahera Hill flora was dominated by woody dicot angiosperm morphotypes. Only one monocot specimen was identified (HW-12) and no herbaceous angiosperm, gymnosperm, or pteridophyte specimens were noted. Additionally, no reproductive material was identified from the site. A complete description of morphotypes from Kiahera Hill is included in the Supplementary Materials.

The preserved flora was comprised entirely of untoothed morphotypes and the average leaf size was mesophyll (Table 2). The average M_A for the flora was 69.3 g m^{-2} (48.3-99.4, Table 2). Using leaf margin analysis and leaf area analysis, MAT and MAP of Kiahera Hill were estimated to be $25 \pm 4.9 \text{ }^{\circ}\text{C}$ and 1812-3577 mm/yr, respectively (Table 2). Using DiLP, MAT and MAP were estimated to be $34.2 \pm 4.0 \text{ }^{\circ}\text{C}$ and 1198-3978 mm/yr (Table 2). Both analyses indicate warm and wet conditions indicating a transitional tropical seasonal forest-tropical rainforest biome (Table 2, Figure 2). The Kiahera Hill flora had a Simpson's index of diversity of 0.38, an average probability of interspecific encounter (PIE) of 0.87, and the rarefied diversity at 50 leaves was 12.96 (Figure 3-4, Table 3).

4.2 R5 Paleoclimate and Paleoenvironment

Maxbauer et al. (2013) identified 16 morphotypes from R5: 14 woody dicots and 2 herbaceous monocots. No gymnosperms, pteridophytes, or angiosperm reproductive structures were identified from the site. The flora was 100% untoothed morphotypes and the average leaf size was microphyll (Table 2). The MAT and MAP of R5 were estimated to be $25 \pm 4.9 \text{ }^{\circ}\text{C}$ and 759-1227 mm/yr, respectively, using univariate methods (Table 2). The average M_A for the flora was

80.1 g m⁻² (68.0-94.3, Table 2). These estimates support the previous interpretation of a woodland biome (Figure 2), however Maxbauer et al. (2013) did not quantitatively estimate paleoclimate or M_A due to small sample size, so these estimates should be interpreted with caution.

Site	Study	MAT (°C)		DiLP (± 4)	MAP (mm)		Maximum leaf area	LAA	Digital leaf area	DiLP	M _A
		P	LMA (± 4.9)		Mean leaf area	LAA					
R3	Michel et al. (2014)	.89	22.8		7.83	1126					
						—					
						2223					
	this study	.93	23.5	29.1	7.98	1199	8.00	1210	7.67	1092	86.3
R5						—		—		—	(60.7-
						2266		2389		3627	122.9)
	Maxbauer et al. (2013)	1.0	25		6.52	759 – 1227					80.1
											(68.0-94.3)
KH	this study	1.0	25	34.2	8.00	1217	8.94	1813	7.90	1198	69.3
						-2401		—		-3978	(48.3-
								3578			99.4)

Table 2. Paleoclimate estimates of the Rusinga Island paleofloras: Kiahera Hill (KH), R5, and R3. Leaf margin analysis (LMA) used the regression from Peppe et al. (2011), leaf area analysis (LAA) used the regression from Jacobs (2002) equation #5, and digital leaf physiognomy used the regression from Peppe et al. (2011).

4.3 R3 Paleoclimate, Paleoenvironment, and Paleoecology

At R3, 52 morphotypes were identified from more than 1500 leaves (Table 1). The majority of the morphotypes were woody dicots. No gymnosperms, pteridophytes, or angiosperm reproductive structures were identified from the site. Leaves were typically preserved separately and were often complete. The R3 flora was spatially variable with monocots and herbaceous taxa, including reed-like morphotypes and emergent aquatics, found dominating patches on the landscape. At AB1805 and AB1806A, which had few or no non-dicot morphotypes, the sediment

was much better cemented than the other floral localities. For a complete list of morphotypes from R3 see the Supplementary Materials.

Sub-locality	Simpson's index of diversity	Probability of interspecific encounter (PIE)	Rarefied diversity at 50 leaves
AB1802C		0.62	7.80
AB1802A		0.63	8.21
AB1802 Combined			8.52
AB1803		0.75	10.25
AB1806		0.78	10.11
AB1806A		0.77	7.87
AB1806 Combined			12.12
<i>Average of R3 sub-localities</i>		<i>0.71</i>	<i>8.85</i>
<i>Combined R3</i>	<i>0.29</i>		
AB1801		0.86	12.66
AB1801A		0.88	13.25
<i>Average of Kiahera Hilltop sub-localities</i>		<i>0.87</i>	<i>12.96</i>
<i>Combined Kiahera Hilltop</i>	<i>0.38</i>		

Table 3. Floral diversity and evenness

The flora was 93% untoothed morphotypes and the average leaf size was microphyll (Table 2). The average M_A for the flora was 86.3 g m^{-2} (60.7-122.9, Table 2). The MAT and MAP of R3 are estimated to be $23.5 \pm 4.9^\circ\text{C}$ and 1210-2389 mm/yr, respectively, using univariate methods (Table 2). Using DiLP, MAT and MAP were estimated to be $29.1 \pm 4.0^\circ\text{C}$ and 1092-3627 mm/yr (Table 2). These estimates indicate a tropical seasonal forest biome (Figure 2). These new estimates are slightly warmer and wetter than previously reported in Michel et al. (2014) (Table 2).

The R3 flora had a Simpson's index of diversity of 0.29, an average PIE of 0.71 (individual sub-localities ranged from 0.62-0.78), and the site average rarefied richness at 50 leaves was 8.85 (individual sub-localities ranged from 7.80-12.12) (Table 3, Figures 3-4). To examine lateral

plant heterogeneity within R3, we calculated Jaccard dissimilarity between sub-localities (Table 4), which measures differences based upon species compositions and frequencies. The mean Jaccard dissimilarity between sub-localities is 0.45, which indicates a relatively heterogenous flora.

Figure 2. Modern ecosystem plots with paleoclimate variables calculated using leaf margin analysis (LMA) and leaf area analysis (LAA). The Kiahera Hill flora (blue square) corresponded with a modern tropical seasonal forest-tropical rainforest. The R3 flora (orange triangle) corresponded with a modern tropical seasonal forest. The R5 flora (green circle) corresponded to a modern woodland. Boxes indicate error estimates for temperature and precipitation.

Figure 3. Rarefaction curves from five census localities in the Early Miocene Hiwegi Formation; envelopes indicate 95% confidence intervals. Blue curves indicate Kiahera Hill localities and orange curves indicate R3 localities.

	AB1802	AB1803	AB1806	AB1806A	Kiahera Hill
AB1802	—	—	—	—	—
AB1803	0.44	—	—	—	—
AB1806	0.44	0.44	—	—	—
AB1806A	0.47	0.48	0.42	—	—
R3 Combined	—	—	—	—	0.76

Table 4. Jaccard dissimilarity using presence/absence data

5. Discussion

5.1 Hiwegi Formation Paleoclimate and Paleoenvironment

The temporal and spatial distributions of the Kiahera Hill and R3 floras allow for relatively high-resolution interpretations of the paleoclimate, paleoenvironment, and paleoecology of Rusinga Island during the Early Miocene. At Kiahera Hill, the flora is dominated in morphotype

composition and abundance by woody dicot angiosperm morphotypes. This dominance may be partially due to the taphonomy of the site, in which many fossil leaves were fragmentary and in preserved in leaf mats. The fragmentary nature of the fossils suggests some degree of transport and it is likely that herbaceous taxa would not have been hardy enough to survive deposition (Burnham 1989, 1994). However, despite these taxonomic constraints, the relatively large collection size suggests that monocot angiosperms were uncommon, and gymnosperms and pteridosperms were very rare to completely absent on the landscape.

Figure 4. Rarefaction curves comparing the number of angiosperm leaf morphotypes at R3 and Kiahera Hill sites. The blue curve indicates Kiahera Hill and the orange curve indicates R3.

All of our diversity, paleoenvironmental, and paleoclimate analyses suggest that the Kiahera Hill flora sampled a tropical rainforest to tropical seasonal forest biome. The MAT and MAP estimates indicate a warm and wet climate, most similar to modern tropical rainforests and tropical seasonal forests (Table 2, Figure 2). Further, comparisons of Kiahera Hill to modern African woodlands, tropical seasonal forests and tropical rainforests suggests that the fossil flora most closely resembles tropical rainforests based on the proportion of untoothed species, the average leaf size, and the M_A (Table 5). The distribution of M_A is similar to modern tropical rainforests and tropical seasonal forests, and most closely resembles tropical rainforests near Monrovia, Liberia and Kakamega, Kenya and a tropical seasonal forest near Abidjan, Côte d'Ivoire (Figure 5). Kiahera Hill has relatively high species richness, evenness, and diversity (Simpson's index of diversity, rarefied richness, PIE) suggesting it likely would have resembled modern rainforests in West and Central Africa (Table 3).

The R3 site is the best studied fossil floral locality in this study. Previous publications reported preliminary paleobotanical interpretations based on a relatively small sample of fossil leaves from the site, and we have made some revisions to the morphotype list and paleoclimate reconstructions presented in Michel et al. (2014) (Table 2). Based on the relatively complete preservation of the fossil leaves, we interpret them to have experienced relatively little transport before deposition. The R3 floras was dominated by woody dicot angiosperms in both abundance and the number of morphotypes across the site. However, it is important to note that monocots and aquatic dicot angiosperms were very common in some of our sub-locality census collections (Table 6) and that monocot morphotypes were recognizable from much smaller fragments than dicot morphotypes, which probably inflated their relative abundance in our census collections.

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Site	Biome	<i>P</i>	MAT (°C)	Average leaf size	MAP (mm)	M _A
Lome, Togo	Woodland	.92	26.8	7.78 notophyll	861	78.6 (51.0 – 113.7)
Dar es Salaam, Tanzania	Woodland	.93	25.9	7.46 microphyll	1046	87.7 (55.7 – 127.9)
Niokolo-Koba, Senegal	Woodland	1.0	28.2	8.05 notophyll	1000	76.7 (50.0 – 118.3)
Entebbe, Uganda	Tropical Seasonal Forest	.81	21.6	8.25 notophyll	1507	77.9 (49.3 – 105.0)
Omo, Nigeria	Tropical Seasonal Forest	.86	26.1	8.53 mesophyll	1800	65.4 (38.1 – 106.0)
Abidjan, Côte d'Ivoire	Tropical Seasonal Forest	.92	26.7	7.92 notophyll	1786	79.5 (53.4 – 114.2)
Kibwezi, Kenya	Tropical Seasonal Forest	.93	21.2	7.44 microphyll	1298	120.8 (61.9 – 223.8)
Cross River, Nigeria	Tropical Seasonal Forest	.93	25.4	8.66 mesophyll	2222	70.5 (45.5 – 102.5)
Lubumbashi, DRC	Tropical Seasonal Forest	.94	20.2	7.49 microphyll	1235	107.9 (70.3 – 154.7)
Mbandaka, DRC	Tropical Seasonal Forest	.96	25.5	8.04 notophyll	1676	79.9 (57.0 – 118.7)
Gola, Senegal	Tropical Seasonal Forest	1.0	25.8	7.99 notophyll	2687	74.1 (44.1 – 99.2)
Kakamega, Kenya	Tropical Rain Forest	.72	20.1	8.09 notophyll	1926	72.3 (47.0 – 116.5)
Banyong, Cameroon	Tropical Rain Forest	.96	19.5	8.96 mesophyll	2600	68.6 (41.3 – 192.7)
Monrovia, Liberia	Tropical Rain Forest	.97	25.7	8.26 notophyll	3316	73.5 (29.1 – 109.5)

467 Table 5. Modern Africa woodlands, tropical seasonal forests and tropical rainforests

Figure 5. Comparison of Kiahra Hill floral leaf mass per area distribution with representative modern sites with different modern African floras (modern biome data from unpublished data). Red bars represent tropical rainforests and orange bars represent tropical seasonal forests. The leaf mass per area distribution of the Kiahra Hill flora is most similar to tropical seasonal forests and tropical rainforest, in agreement with the paleoclimate estimates, which indicate a transitional tropical seasonal forest-tropical rainforest.

Plant group	Subgroup	# Morphotypes	% Morphotypes	% AB180 2 Census	% AB180 3 Census	% AB180 6 Census	% AB1806 A Census	% Total Census
Monocotyledonous angiosperms	Emergent aquatic	3	6	77	48	62	4	56
Dicotyledonous angiosperms		49	94	23	52	38	96	44
	Woody	47	90	21	50	37	95	43
	Herbaceous	2	4	2	1	1	2	1
	Emergent aquatic	1	2	0	0	0	0	0

Table 6. Number of morphotypes and specimens by category. For morphotype descriptions and illustrations see Supplementary Appendix 1.

Of the 52 morphotypes at R3, only four morphotypes were toothed and the average leaf size at the site was relatively large, suggesting warm and wet conditions indicative of a tropical seasonal forest to woodland biome (Table 2; Figure 2). The R3 reconstructions of MAT and MAP

were lower than Kiahira Hill (Table 2; Figure 2). Comparing R3 to modern African environments suggests that the fossil flora had similarities to modern woodlands and tropical seasonal forests and the distribution of M_A was similar to tropical seasonal forests near Abidjan, Côte d'Ivoire and Kibwezi, Kenya (Table 5, Figure 6). R3 had lower diversity (Simpson's index of diversity and rarefied diversity) and lower evenness (PIE) than Kiahira Hill (Table 3).

Figure 6. Comparison of R3 floral leaf mass per area distribution with representative modern sites with different modern African floras (modern biome data from unpublished data). Yellow bars represent woodlands and orange bars represent tropical seasonal forests. The leaf mass per area distribution of the R3 flora is most similar to tropical seasonal forests, in agreement with the paleoclimate estimates, which indicate a tropical seasonal forest.

Floral collections from across the R3 site indicate that the environment was heterogeneous (Table 4), with some sites only preserving woody dicot leaves and others preserving the leaves of woody dicots, as well as monocots and emergent aquatic dicots (Table 6). This spatial heterogeneity in the floras was previously described by Michel et al. (2014), who also noted abundant *in situ* tree stump casts, which were interpreted to indicate an interlocking or

overlapping canopy. Interestingly, the stump casts were not evenly distributed across the site, and some locations have relatively few stump casts whereas other locations had many closely spaced stump casts. Our fossil leaf collections closer to the abundant, closely spaced stump casts were dominated by woody dicot leaves (e.g., AB1805). In contrast, our collections with few preserved stump casts had woody dicot leaves, as well as common monocots and emergent aquatic dicots (e.g., AB1802). This suggests that the areas with few stump casts were more open locations on the landscape where there was periodic ponding leading to patches of reed-like monocots and emergent aquatics. In addition, the locations with few stump casts preserve grass phytoliths, which also indicate more open environments (Novello et al., 2016). Macromorphological features of paleosols indicate seasonal precipitation with distinct dry and wet periods, and the horizontal habit of the roots indicates a shallow water table (Michel et al. 2014). Taken together, these results demonstrate that R3 had both locations on the landscape that were closed forest with an interlocking canopy and locations that were more open and perhaps covered by small ponds or standing water in the wet season with grasses, reed-like monocots, and emergent aquatic dicots. Given the evidence for seasonal precipitation, we suggest that the spatial heterogeneity at R3 could have been maintained by ponding during the wet season.

The R5 flora stands in sharp contrast to the Kiahara Hill and R3 floras in plant community composition and paleoenvironment. Maxbauer et al. (2013) did not make census collections from R5, making it impossible to quantitatively compare the diversity or evenness to the other fossil floras in this study. However, qualitative comparisons are informative. Like the Kiahara Hill and R3 floras, the R5 flora was dominated by woody dicot morphotypes (14 dicots, 2 monocots). However, the two monocot morphotypes (HW-09 and HW-12) were two of the

most abundant morphotypes in the flora in terms of collected specimens. All of the woody dicots in the R5 flora were untoothed indicating very warm temperatures, and the average leaf size suggests a moderate amount of precipitation (Table 2, Figure 2). The presence of salt-hoppers overlying the R5 leaf layers indicate episodic dry periods where evaporation exceeded precipitation. The average leaf size of the flora, the taxonomic affinities of the monocots, coupled with fluvial sedimentary structures was used to interpret the R5 flora as a periodically flooded riparian woodland environment (Maxbauer et al. 2013), which is supported by the paleoclimate reconstructions based on the fossil leaves (Figure 2). The vertebrate fauna, which include a crocodilian bonebed, hippopotamuses and rhinoceroses, as well as primates, also indicate episodic standing water and riparian woodland with both more open and more closed habitats in close proximity on the landscape (Conrad et al. 2013; Maxbauer et al. 2013). These analyses demonstrate that the R5 flora had a similar mean annual temperature but was notably drier than the Kiahera Hill and R3 floras (Figure 2).

Comparisons of the Kiahera Hill, R5, and R3 floras provide evidence of dramatic paleoclimate and paleoenvironmental change on Rusinga Island during the Early Miocene, as well as significant changes in plant community composition. Kiahera Hill, the oldest flora in the Hiwegi Formation, is interpreted to have been similar to a modern tropical rainforest or tropical seasonal forest. The Kiahera Hill flora climate reconstructions suggest that it sampled the warmest and wettest interval in the Hiwegi Formation (Figure 2; Table 2). The average M_A and the distribution across all taxa were most similar to modern tropical rainforests from equatorial Africa (Table 5, Figure 5). Interestingly, the average M_A of Kiahera Hill was lower than that of R3, which we interpret to have been similar to a tropical seasonal forest, and similar to the

pattern of M_A seen in modern African tropical rainforests and tropical seasonal forests (Table 5; Figures 5-6). The Kiahera Hill flora was also more diverse and more even than R₃, but had a lower species richness (Table 3, Figures 3-4) and the floral composition of the sites was very different (Table 4).

Qualitatively, the morphotype composition of the Kiahera Hill flora is notably different from R₅ and R₃, suggesting considerable changes in plant community composition between the floras, and particularly between Kiahera Hill and R₅. Of the 40 morphotypes found at Kiahera Hill, 63% were unique to that flora (Table 7). Kiahera Hill shared 5 morphotypes with R₅ and 13 with R₃; 3 morphotypes found at Kiahera Hill were identified at all three sites. R₅ was a riparian woodland environment, so it is not surprising that Kiahera Hill shared fewer morphotypes with R₅ than R₃, as the Kiahera Hill and R₃ floras were both tropical forests (Figure 2).

Site	Total Morphotypes	% Unique Morphotypes	Kiahera Hill	R ₅	# All Sites
R ₃	52	71	13	5	3
R ₅	16	56	5	—	
Kiahera Hill	40	63	—		

Table 7. Number of morphotypes by locality

R₃ is the youngest flora in the Hiwagi Formation and has similarities to both the Kiahera Hill and R₅ floras. The paleoclimate estimates and the relatively high M_A of the R₃ flora demonstrate that the flora was similar to modern African tropical seasonal forest (Table 5, Figures 2, 6). Of the 52 morphotypes found at R₃, 71% were unique to that flora (Table 7). R₃ shared 13 morphotypes with Kiahera Hill and 5 with R₅; 3 morphotypes found at R₃ were identified at all three sites. Given the similar paleoenvironmental reconstructions for Kiahera Hill and R₃ (tropical forest), it is not surprising that they would share many of the same morphotypes.

However, it is very interesting to note that the Kiahera Hill flora is approximately 500 kyr older than the R3 flora (Peppe et al. 2016), and the plant composition of both floras is remarkably different from that of the intervening R5 flora. The R5 flora was reconstructed to be much drier and more open than the Kiahera Hill and R3 floras (Figure 2), and it is unsurprising that we document changes between the floras, particularly since many tropical plant taxa are environmentally sensitive. Interestingly, 10 morphotypes that disappear between the Kiahera Hill and R5 floras return again in the R3 flora, suggesting that they may have been locally expatriated in response to the environmental changes.

5.2 Comparisons to Previous Work

For nearly 70 years, paleontologists have attempted to reconstruct the paleoenvironment of the Hiwegi Formation using qualitative and quantitative methods (i.e. faunal analysis, paleobotany, geochemistry, paleopedology) and estimates have ranged from tropical rainforests to semi-arid environments (e.g., Chesters 1957; Andrews and Van Couvering 1975; Evans et al. 1981; Collinson 1985; Thackray 1994; Retallack et al. 1995; Bestland and Krull 1999; Forbes et al. 2004; Collinson et al. 2009; Ungar et al. 2012; Maxbauer et al. 2013; Michel et al. 2014). Previous estimates that focused on the entirety of the Hiwegi Formation were likely time-averaged and imprecise due to sampling multiple paleoenvironments, so for the sake of comparison we will focus on studies that sampled discrete time intervals (e.g., Collinson 1985; Thackray 1994; Collinson et al. 2009; Maxbauer et al. 2013; Michel et al. 2014, in press).

Paleobotanical analyses of R117 in the Grit/Fossil Bed Member by Collinson (1985) and Collinson et al. (2009) applied NLR methods to fruits, seeds, and wood and interpreted the

paleoenvironment as a woodland with nearby forest. Spatially and temporally, R117 is closest to R5, which has also been interpreted as a riparian woodland environment (Maxbauer et al. 2013). However, it is important to note that NLR methods, which use the inferred closest modern relative's climatic and environmental tolerances to reconstruct paleoenvironment and paleoclimate, become less reliable in older fossil assemblages (Grimm and Denk 2012; Peppe et al. 2018). Unlike leaf physiognomic paleoclimate methods, which use the functional relationship between leaf size and shape and climate to estimate paleoclimate, NLR methods assume that a taxonomic group's climatic tolerances remain unchanged through time. Nonetheless, the results of previous work (Collinson 1985; Collinson et al. 2009; Maxbauer et al. 2013) and our analyses for the Grit/Fossil Bed Member of the Hiwegi Formation indicate that it was a drier climate with a more open environment.

Like plants, small animals can be reliable paleoclimatic and paleoenvironmental indicators due to their relative spatial restriction. Thackray (1994) described a fossil nest of sweat bees (Halictinae) from the Kibanga Member and concluded that it indicated a sub-humid to humid climate and angiosperm-dominated vegetation. Spatially and temporally, this site is closest to R3, and the paleoenvironmental reconstruction is very similar to the reconstruction for R3, which is interpreted to have been a closed canopy tropical seasonal forest with more open patches that periodically had standing water (Michel et al. 2014; this study).

Taken together, our results and comparisons of site-specific studies through the Hiwegi Formation supports the conclusions of Michel et al. (in press) that the Hiwegi Formation was environmentally variable, with a warm and wet, closed environment during the Kaswanga Point

Member transitioning to a relatively dry and open environment during the Grit/Fossil Bed Member followed by a wetter and more closed environment during the Kibanga Member. Based on our paleobotanical paleoclimate reconstructions, we conclude that though the temperature on Rusinga Island was relatively consistent throughout the Hiwegi Formation, precipitation was considerably variable, and this variability was the driving factor of paleoenvironmental change. It has been demonstrated that the fossil apes on Rusinga Island lived in a variety of habitats (e.g., Retallack et al. 1995; Peppe et al. 2009; Maxbauer et al. 2013; Michel et al. 2014), and this ability to weather environmental variability was likely crucial to the evolution and habitat preferences of early hominoids.

5.3 Early Miocene Regional Paleoenvironment and Implications for Hominoid Evolution

There is a longstanding paradigm that a “pan-African” lowland forest persisted during the Early Miocene that transitioned to a mosaic of open and closed environments during the Middle Miocene (e.g., Chesters 1957; Hamilton 1968; Wichura et al. 2015). However, the pattern in East Africa appears to be more complicated.

The Oligo-Miocene of the Turkana Basin has been reconstructed as a mosaic of semi-deciduous forests and woodlands (Vincens et al. 2006) and in the Mush Valley, Ethiopia moist tropical forests were present during the Early Miocene (Jacobs et al. 2010; Pan et al. 2012; Bush et al. 2017; Currano et al. 2020). Environmental reconstructions of Moroto, Uganda indicate a mosaic of closed-canopy forests and open habitat (Kingston 2007; Kingston et al. 2011). Localities at Tinderet have been reconstructed as forested environments, with the Koru site being slightly wetter than Songhor (e.g., Andrews et al. 1997; Ungar et al. 2012; Oginga et al. 2017).

Karungu, near Rusinga Island, has been reconstructed as a dynamic seasonal paleoenvironment that ranged from riparian woodland to wooded grassland (Driese et al. 2016; Lukens et al. 2017). Kalodirr and Moruorot, near Lake Turkana, have been reconstructed as a seasonally wet woodland (Leakey and Leakey 1986; Grossman and Holroyd 2009; Orliac 2009; Leakey et al. 2011; Grossman and Solounias 2014). Our results from Rusinga Island, combined with previous research (e.g., Collinson 1985; Thackray 1994; Collinson et al. 2009; Maxbauer et al. 2013; Michel et al. 2014, in press) demonstrates considerable environmental variability between more open woodlands and more closed tropical forests through the ~500 kyr depositional history of the Hiwegi Formation. Therefore, it is clear that while forests were common in East Africa during the Early Miocene, they were not ubiquitous.

Rather than a “pan-African forest”, it is instead more likely that during the Early Miocene a mosaic landscape of open and closed environments spread across East Africa, much like Africa today (e.g., White 1985; Mayaux et al. 2004). This reinterpretation of the traditional hypothesis is central to providing the proper context for hominoid evolution (Linder 2017). It is becoming increasingly evident based on work at Rukwa (Stevens et al. 2013), Karungu (Driese et al. 2016; Lukens et al. 2017), Rusinga Island (Collinson, 1985; Collinson et al., 2009; Maxbauer et al., 2013; Michel et al in press, this study), and Loperot (Liutkus-Pierce et al. 2019) that early apes were not restricted to forested environments, and also commonly occurred in more open woodland environments. The distinction between woodlands and forests is important because, though both habitat types are tree dominated, the density and structure of vegetation differs dramatically (Jacobs 2004; Reed and Bidner 2004). Continued paleobotanical work in the region is necessary to provide the context for the evolution of early apes.

6. Conclusions

The paleofloras of the Early Miocene Hiwegi Formation support previous interpretations of temporal environmental heterogeneity on Rusinga Island. The Kiahera Hill flora in the Kaswanga Point Member was a warm and wet, closed forest, followed by a relatively dry and open environment in the Grit/Fossil Bed Member at R5 and a wetter and spatially heterogeneous forest at R3 in the Kibanga Member. Floral composition of these fossil sites differed dramatically but Kiahera Hill and R3 were more similar to each other than either flora was to R5. The absence of morphotypes from the R5 flora that were present in the Kiahera Hill and R3 floras provides evidence for local extirpation during the R5 time interval. Based on our paleobotanical paleoclimate reconstructions, we conclude that environmental variability was driven by changes in precipitation but not temperature. These results from Rusinga Island provide important context for the evolution and habitat preference of early apes and suggest that the paleoenvironment of the Early Miocene was variable both spatially and temporally.

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