

Taxonomy and Biogeography of the Gentle Monkey *Cercopithecus mitis* Wolf, 1822 (Primates: Cercopithecidae) in Kenya and Tanzania, and Designation of a New Subspecies Endemic to Tanzania

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Abstract: The complex taxonomy and biogeography of the highly polytypic and widespread gentle monkey *Cercopithecus mitis* continue to be debated. Tanzania and Kenya, together, support eight of the currently recognized 17 subspecies of *C. mitis*. This paper reviews the taxonomy of the eight subspecies of *C. mitis* recognized for Kenya and Tanzania and presents an overview of their geographic distribution and pelage coloration and pattern. This paper also describes a new, endemic, subspecies of *C. mitis* for Tanzania, offers two hypotheses for its origin and phylogenetic affinities, and assesses its conservation status and conservation needs. *Cercopithecus mitis* in the Lake Manyara-Ngorongoro Region of central north Tanzania (i.e., the “Manyara Population”) has often been referred to as “*C. m. stuhlmanni* × *C. m. albogularis* hybrids” and as representative of a “hybrid swarm.” To better understand the taxonomic and conservation status of this population, four field surveys totaling 25 days were undertaken in southwest Kenya and central north Tanzania. The aim was to determine the geographic distribution of this population and to obtain detailed descriptions and photographs of as many individuals as possible. In addition, the literature was searched, and 88 *C. mitis* specimen skins were directly examined at four museums. We found no evidence to support the contention that *C. mitis* of the Lake Manyara-Ngorongoro Region are hybrids or represent a hybrid swarm. The Manyara *C. mitis* is geographically isolated from other *C. mitis* by >90 km of semi-arid habitat, is phenotypically distinct from other *C. mitis*, and presents little intra-population variation. As such, the diagnosable phenotypic characters of this population appear to be fixed, genetic, and heritable. In this paper we describe a new subspecies of *C. mitis*, the “Manyara monkey.” The holotype, an adult female skin at the Natural History Museum, London, was collected by B. Cooper in 1937 at the north end of Lake Manyara. Two paratopotypes are also designated. This *Cercopithecus mitis* ssp. nov. is endemic to central north Tanzania. The known geographic distribution extends from the Ngorongoro Conservation Area southwards through Lake Manyara National Park to the Nou Catchment Forest Reserve and Ufiome Forest Reserve. The known geographic distribution is c. 1,480 km², while the probable geographic distribution is c. 5,865 km². This monkey occupies various types of forest from 960 m asl to at least 2,550 m asl, while the probable upper limit is c. 3,260 m asl. Mean annual rainfall across the known and probable geographic distribution ranges from c. 500 mm to c. 1,200 mm. *Cercopithecus mitis* ssp. nov. appears to represent a relic population. We put forth two hypotheses for its origin. Hypothesis I: It represents a now isolated section of a phenotypic cline that once extended across the Eastern Rift Valley. Hypothesis II: It is a close relative of *C. m. opisthostictus* and, thereby, is a relic of dispersal from the Congo Basin/Upper Zambezi Basin to the Lake Manyara-Ngorongoro Region. Additional biogeographical research and, particularly, deep molecular research are required to further our understanding of the taxonomy and evolutionary history of *C. mitis*. Although c. 60% (c. 3,500 km²) of the probable geographic distribution of this *C. mitis* ssp. nov. lies within six protected areas, the future of this monkey is uncertain due to threats associated with the region’s rapidly increasing human population, particularly the degradation, loss, and fragmentation of forest. When assessed in 2016 as *C. mitis* ssp. nov. for the IUCN Red List of Threatened Species, the threat category designated was Endangered. Conservation priorities for this new subspecies include the effective management of the six protected areas in which it occurs and the restoration and protection of the wildlife corridors of the Lake Manyara-Ngorongoro Region.

Résumé: La taxonomie et la biogéographie complexes du cercopithèque à diadème *Cercopithecus mitis*, une espèce polytypique et répandue, continuent de faire l’objet de discussions. La Tanzanie et le Kenya abritent ensemble huit des 17 sous-espèces de *C. mitis* reconnues aujourd’hui. Ce document examine la taxonomie des huit sous-espèces de *C. mitis* reconnues pour le Kenya et la Tanzanie et présente un aperçu de leur distribution géographique et des colorations et motifs de leur pelage. Cet article décrit également une nouvelle sous-espèce endémique de *C. mitis* de Tanzanie, présente deux hypothèses quant à son origine et ses affinités phylogénétiques et évalue son statut et ses besoins en matière de conservation. Dans la région du lac Manyara-Ngorongoro dans le centre-nord de la Tanzanie (« la population de Manyara »), les individus de *Cercopithecus mitis* ont souvent été qualifiés d’« hybrides » de *C. m. stuhlmanni* × *C. m. albogularis* et de représentants d’un « essaim d’hybrides ». Quatre

inventaires de terrain d'une durée totale de 25 jours ont été réalisés dans le sud-ouest du Kenya et dans le centre-nord de la Tanzanie afin de mieux appréhender le statut taxonomique et de conservation de cette population. L'objectif était de déterminer sa distribution géographique et d'obtenir des descriptions détaillées et des photographies du plus grand nombre possible d'individus. En outre, une recherche documentaire a été effectuée et 88 peaux de spécimens de *C. mitis* ont été examinées dans quatre musées. Nous n'avons trouvé aucune preuve permettant d'appuyer l'affirmation que les individus de *C. mitis* de la région du lac Manyara-Ngorongoro sont des hybrides ou représentent un essaim d'hybrides. Les individus de *C. mitis* de Manyara sont isolés géographiquement des autres individus de *C. mitis* par plus de 90 km d'habitat semi-aride, sont phénotypiquement distincts des autres individus de *C. mitis* et présentent peu de variation intra-populationnelle. Par conséquent, les caractéristiques phénotypiques diagnosticables de cette population semblent être fixes, génétiques et héréditaires. Nous décrivons dans ce document une nouvelle sous-espèce de *C. mitis*, le « Cercopithèque de Manyara ». L'holotype, la peau d'une femelle adulte se trouvant au Natural History Museum de Londres, a été collecté par B. Cooper en 1937 à l'extrémité nord du lac Manyara. Deux para-topotypes sont aussi nommés. Cette sous-espèce, *Cercopithecus mitis* ssp. nov., est endémique du centre-nord de la Tanzanie. La distribution géographique connue s'étend de la zone de conservation du Ngorongoro vers le sud, couvre le parc national du lac Manyara jusqu'à la réserve forestière du bassin hydrographique de Nou et la réserve forestière d'Ufiome. La distribution géographique actuellement connue est d'environ 1480 km², alors que la distribution géographique probable est d'environ 5,865 km². Ce singe est présent dans différents types de forêt de 960 m d'altitude à au moins 2550 m, la limite supérieure d'altitude probable étant d'environ 3260 m. La pluviométrie annuelle moyenne dans l'aire de distribution géographique probable varie entre environ 500 mm et 1200 mm. *Cercopithecus mitis* ssp. nov. semble représenter une population relique. Nous avançons deux hypothèses quant à son origine. Hypothèse I : elle représente une section aujourd'hui isolée d'un cline phénotypique qui s'étendait autrefois dans la partie orientale de la vallée du Rift. Hypothèse II : elle est étroitement apparentée à *C. m. opisthostictus* et est donc une relique d'une dispersion du bassin du Congo/du bassin du Zambèze supérieur vers la région du lac Manyara-Ngorongoro. Des recherches biogéographiques supplémentaires, et, en particulier, des recherches moléculaires approfondies, sont requises pour mieux comprendre la taxonomie et l'histoire évolutive de *C. mitis*. Même si environ 60% (3500 km²) de l'aire de distribution géographique probable de *C. mitis* ssp. nov. se trouve au sein de six aires protégées, l'avenir de ce singe est incertain en raison des menaces associées à la croissance rapide de la population humaine dans la région, en particulier la dégradation, la disparition et la fragmentation de la forêt. Lorsque son statut a été évalué en 2016 en tant que *C. mitis* ssp. nov. pour la Liste rouge des espèces menacées de l'UICN, il a été placé dans la catégorie « En danger ». Les priorités pour la conservation de cette nouvelle sous-espèce comprennent la gestion efficace des six aires protégées où elle est présente, ainsi que la restauration et la protection des corridors fauniques de la région du lac Manyara-Ngorongoro.

Key Words: *Cercopithecus mitis* ssp. nov., conservation, hybrid swarm, hybrid zone, Lake Manyara, Manyara monkey, Ngorongoro

Introduction

The gentle monkey *Cercopithecus mitis* Wolf, 1822 is a widespread species endemic to sub-Saharan Africa, and the only forest-dependent guenon (tribe Cercopithecini) with a wide distribution in eastern and southern Africa. This species is the most ecologically diverse member of its genus, occupying many types of primary and secondary forest, including riparian, gallery, swamp, mangrove, coastal, groundwater, lowland, mid-altitude (= transitional), montane, and bamboo forest (Kingdon 1971; Butynski 1990; Lawes 1990; Lawes *et al.* 2013). Unlike other *Cercopithecus* spp., *C. mitis* is tolerant of poor-quality habitats (Lawes 1990), including suburban areas with wooded gardens near forest, and occurs over a wide altitudinal range (0–3,800 m above sea level [asl]; Lawes *et al.* 2013; De Jong and Butynski 2018; see below). Despite the eurytopic ecology of *C. mitis*, arid and semi-arid habitats (e.g., deserts, grasslands, bushlands, open woodlands) are geographic barriers. This, together with

big rivers and big lakes, largely explains the current fragmented geographic distribution of *C. mitis*, as well as the great variation present in the coloration and pattern of the pelage (Kingdon 2013; Lawes *et al.* 2013; De Jong and Butynski 2018).

Cercopithecus mitis is a highly polytypic species with a particularly complex and extensively debated taxonomy (Pocock 1907; Elliot 1913; Allen 1925, 1939; Schwarz 1928, 1954; Booth 1962, 1968; Hill 1966; Kuhn 1967; Napier and Napier 1967; Rahm 1970; Thorington and Groves 1970; Kingdon 1971, 1997, 2013, 2015; Dandelot 1974 [not 1971, as sometimes cited]; Napier 1981; Lernould 1988; Groves 1993, 2001, 2005; Grubb 2001; Butynski 2002; Grubb *et al.* 2003; Lawes *et al.* 2013; Zinner *et al.* 2013a; Lo Bianco *et al.* 2017; De Jong and Butynski 2018). The phenotypic diversity of *C. mitis* is unprecedented among African primates. At present, 17 subspecies are recognized, under which no fewer than 28 major synonyms have been placed (Lawes *et al.* 2013). The classification of subspecies within *C. mitis* is mainly

founded on geographic distribution and pelage coloration and pattern, although a few preliminary genetic studies have been conducted that examine the subspecies-level taxonomy and phylogeny of *C. mitis* (Turner *et al.* 1988; Guschanski *et al.* 2013; Dalton *et al.* 2015).

Documenting the morphological variation and biogeography of a rapidly radiating, highly polytypic, taxonomically complex, and fossil-poor species such as *C. mitis* is necessary for a better understanding of its evolutionary history, phylogeny, and current evolutionary trajectories. Here, we review the taxonomy of the eight subspecies of *C. mitis* currently recognized for Kenya and Tanzania and present an overview of their geographic distribution and pelage coloration and patterns. We also describe a new subspecies of *C. mitis* endemic to Tanzania, offer hypotheses for its origin and phylogenetic affinities, and assess its conservation status and conservation needs.

Cercopithecus (nictitans) Superspecies and Cercopithecus mitis/albogularis Subgroup

The “Nictitans Monkeys Superspecies *Cercopithecus (nictitans)*” refers to a large and complex group of guenons that is distributed across Africa from the Atlantic Ocean (Liberia) to the Indian Ocean (Zanzibar Island [= Unguja Island] and Mafia Island, east Tanzania), and from southwest Ethiopia to near the southern tip of South Africa (Hill 1966; Dandelot 1974; Lerno 1988; Kingdon 1997, 2013, 2015; Grubb *et al.* 2003; Lawes *et al.* 2013). This Superspecies includes the “Putty-nosed Monkeys *Cercopithecus nictitans* Subgroup” and the “Gentle Monkeys *Cercopithecus mitis/albogularis* Subgroup” (Kingdon 1997, 2013, 2015; Grubb *et al.* 2003; Lawes *et al.* 2013). While 52 forms have been described and named in the *C. (nictitans)* Superspecies, current taxonomy recognizes 19–21 subspecies of two species; *Cercopithecus nictitans* (Linnaeus, 1766) and *Cercopithecus mitis*. Several “sections” (= “clusters” = “subspecies groups”) are recognized in the *C. mitis/albogularis* Subgroup (Napier 1981; Kingdon 1997, 2013, 2015; Grubb 2001; Grubb *et al.* 2003; Lawes *et al.* 2013). Kingdon (2013, 2015) recognizes six sections, while Grubb *et al.* (2003) and Lawes *et al.* (2013) recognize five. Here we follow Grubb *et al.* (2003) and Lawes *et al.* (2013). This is the taxonomy for *C. mitis* adopted at the IUCN SSC African Primate Red List Assessment Workshop in Rome in April 2016 (Butynski and De Jong 2019a).

Subspecies of *Cercopithecus mitis* in Kenya and Tanzania

Eight subspecies in the *Cercopithecus (mitis/albogularis)* Subgroup are currently recognized for Kenya and Tanzania (Figs. 1–3; Table 1; Kingdon 1997,

2013, 2015; Grubb *et al.* 2003; De Jong and Butynski 2012, 2018; Lawes *et al.* 2013; Butynski and De Jong 2019a). Following Kingdon (2013), these fall within the Albogularis Section, Stuhlmanni Section, and Opisthostictus Section. Here are the three sections, their subspecies in East Africa, and the primary diagnostic pelage colors and patterns of adult males. Note that each of the following diagnostic traits will, taken alone, allocate the seven subspecies in the Albogularis and Stuhlmanni Sections to the correct section.

Albogularis Section: *albogularis*, *albotorquatus*, *kolbi*, *moloneyi*, *monoides*. Dark brow-band (= brow-line = diadem) not contrasting in color with crown and not same color as back; distinct fringe of long hair along ear margin; partial white/whitish neck-collar present; crown, nape, neck, and area between shoulders not black; no black band across shoulders; back with gradual increase in rufous wash from shoulders to base of tail; no dark grey or black band across chest; sharp demarcation and moderate color contrast between dark grey ankles and black feet.

Stuhlmanni Section: *doggetti*, *stuhlmanni*. Pale brow-band distinct, contrasting in color with crown and about same color as back; fringe of hair along ear margin relatively indistinct or absent; neck-collar absent; crown, nape, neck, and area between shoulders black; black band across shoulders; back mainly grey flecked black or olive with no rufous; dark grey or black band across chest; little or no demarcation or color contrast between blackish ankles and black feet.

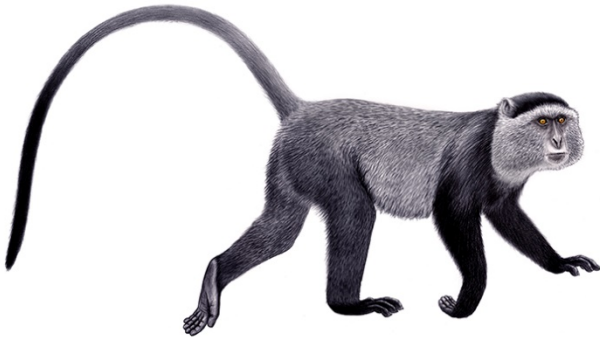
Opisthostictus Section: *opisthostictus*. Crown black or blackish, flecked grey at front; nape and shoulder-band blackish flecked grey; back light grey flecked black and buff giving a pale yellowish-grey appearance; rump with reddish-olive tint; ventrum black or blackish; moderate to high demarcation and color contrast between grey ankles and black feet.

An isolated population of *C. mitis* (Figs. 3 and 4) occurs in central north Tanzania, from the Ngorongoro Conservation Area (CA) southwards through Lake Manyara National Park (NP), Mbulu, Dakakuta Ranch, Nou Catchment Forest Reserve (CFR), and Ufiome FR. This population is hereafter referred to as the “Manyara Population”, and this monkey is hereafter referred to as the “Manyara *C. mitis*” (Figs. 1 and 2).

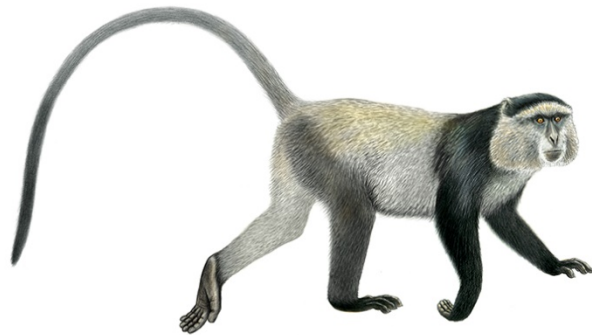
In 1928, I. J. Perkin and O. J. Gromme each collected two specimens from the Manyara Population at Moto Umbu (= Mto wa Mbu), Lake Manyara, that are now at the Field Museum of Natural History, Chicago (accession



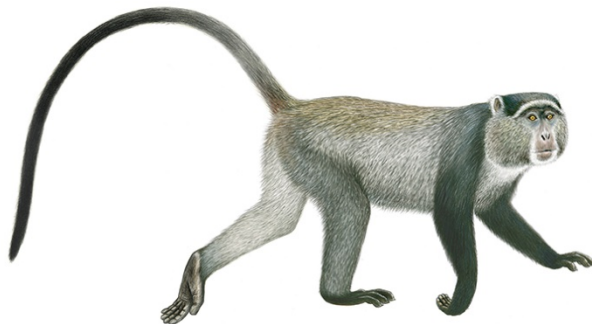
opisthostictus



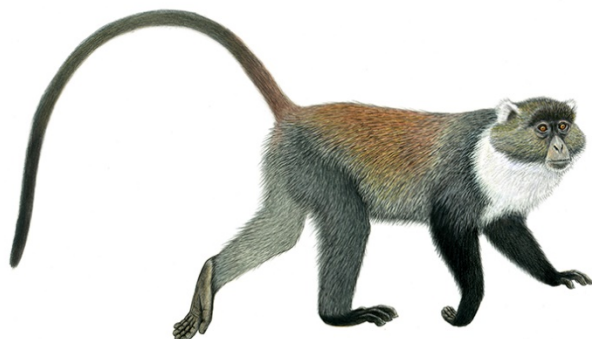
stuhlmanni



doggetti



Manyara
C. mitis



kolbi



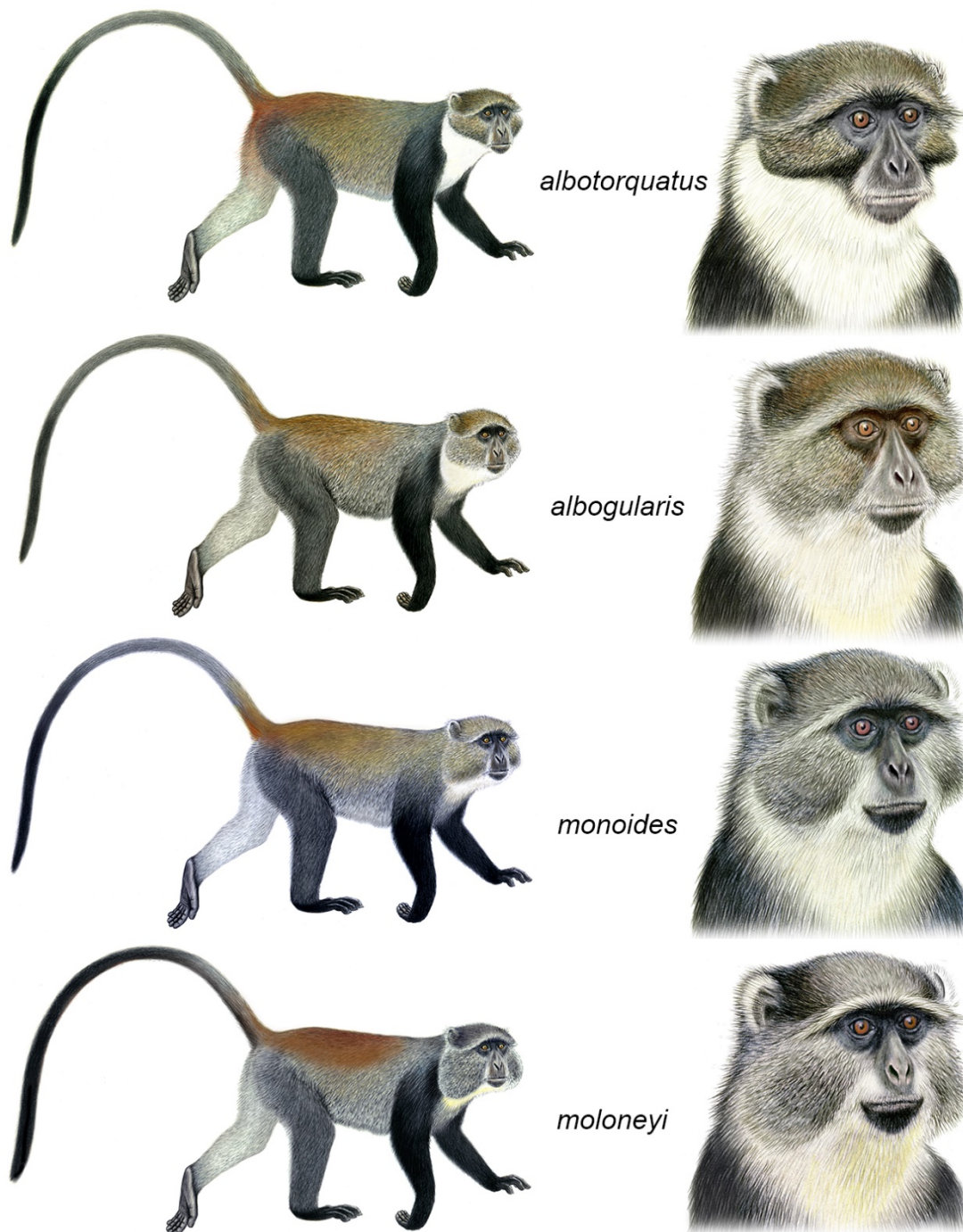
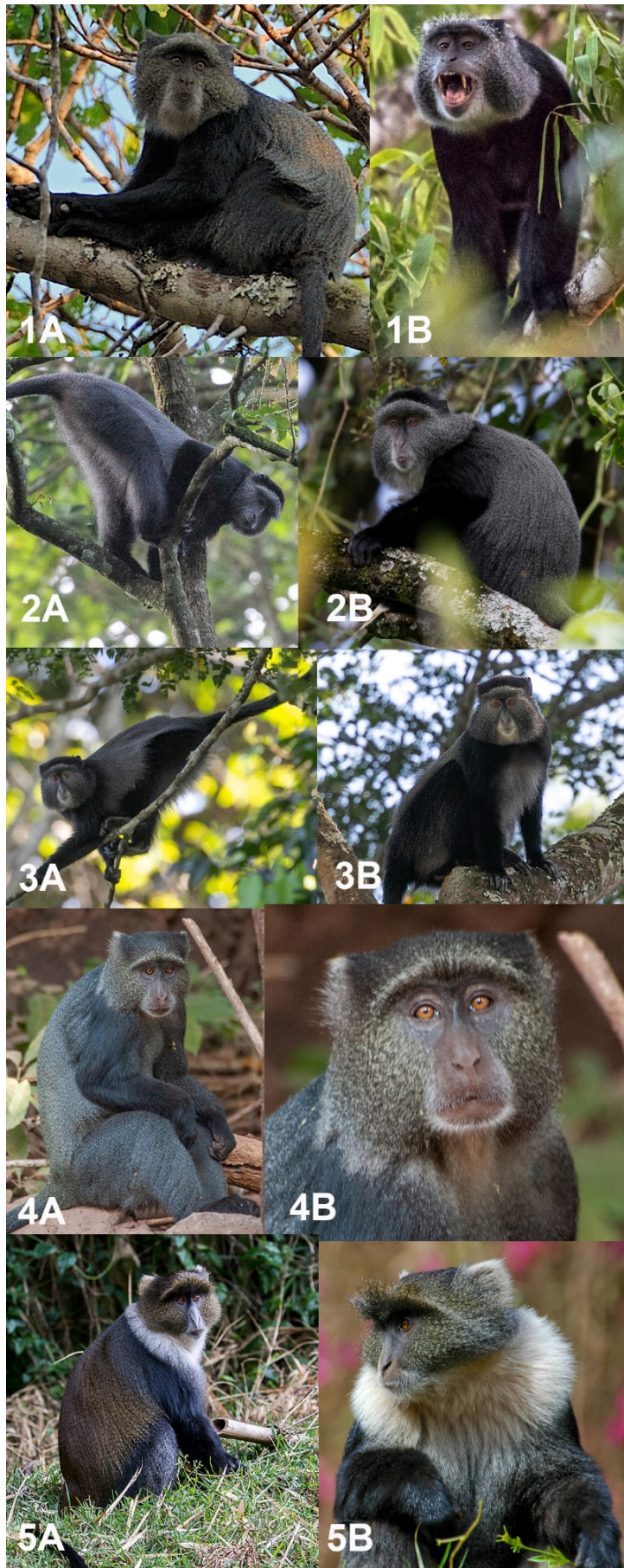


Figure 1. Adult males of the eight subspecies of gentle monkey *Cercopithecus mitis* known to occur in Kenya and Tanzania. Also shown is the *C. mitis* found in the Lake Manyara-Ngorongoro Region. These drawings, and the photographs in Figure 2, demonstrate the rich array of pelage colors and patterns on which the current taxonomy of *C. mitis* is mainly founded. Drawings based on the literature, and on direct observations and photographs of museum specimens and free-living individuals. All drawings of the eight recognized subspecies checked against the original description of the holotype. Drawings by Stephen D. Nash.



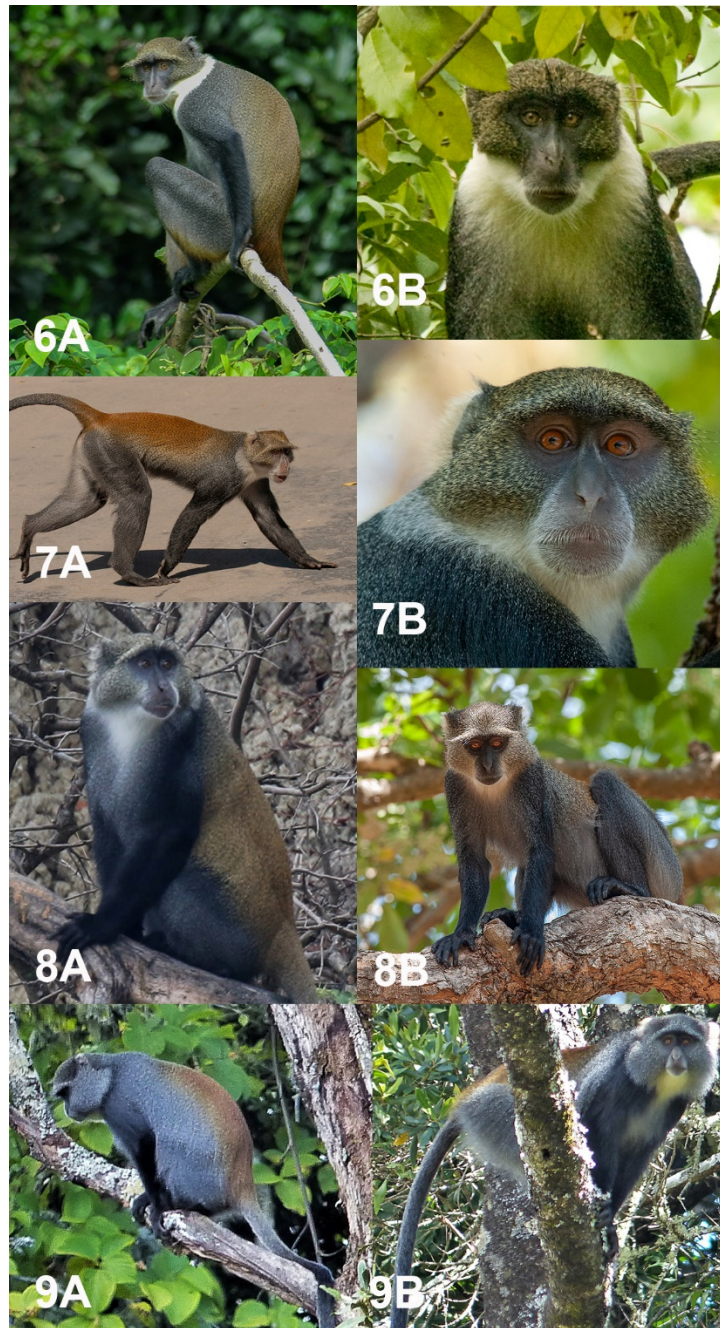


Figure 2. Adult males of the eight subspecies of gentle monkey *Cercopithecus mitis* known to occur in Kenya and Tanzania. Also shown is an adult male *C. mitis* from the Lake Manyara-Ngorongoro Region. All photographs are of free-living individuals. 1A. *opisthostictus*, Nsoba Game Farm, Ndola, central Zambia (photograph by Chris Meyer); 1B. *opisthostictus*, Luombwa River, west Kasanka National Park, central north Zambia (photograph by Fenton Cotterill); 2A. *stuhlmanni*, Kakamega Forest National Reserve, west Kenya; 2B. *stuhlmanni*, Southwest Mau Forest Reserve, southwest Kenya; 3A, B. *doggetti*, Sango Bay, south Uganda; 4A, B. *C. mitis* Lake Manyara National Park, central north Tanzania; 5A. *kolbi*, Aberdare National Park, central Kenya; 5B. *kolbi*, Nairobi National Park, central south Kenya; 6A, B. *albotorquatus*, Witu Forest Reserve, north coast Kenya; 7A, B. *albogularis*, Diani, south coast Kenya; 8A. *monoides*, Rufiji River, central coast east Tanzania (photograph by Martin Grimm); 8B. *monoides*, Selous Game Reserve, central Tanzania (photograph by Dominique Mignard); 9A,B. *moloneyi*, Nyika National Park, north Malawi (photographs by Eleanor Darbey). Unless otherwise stated, photographs by Yvonne de Jong and Tom Butynski.

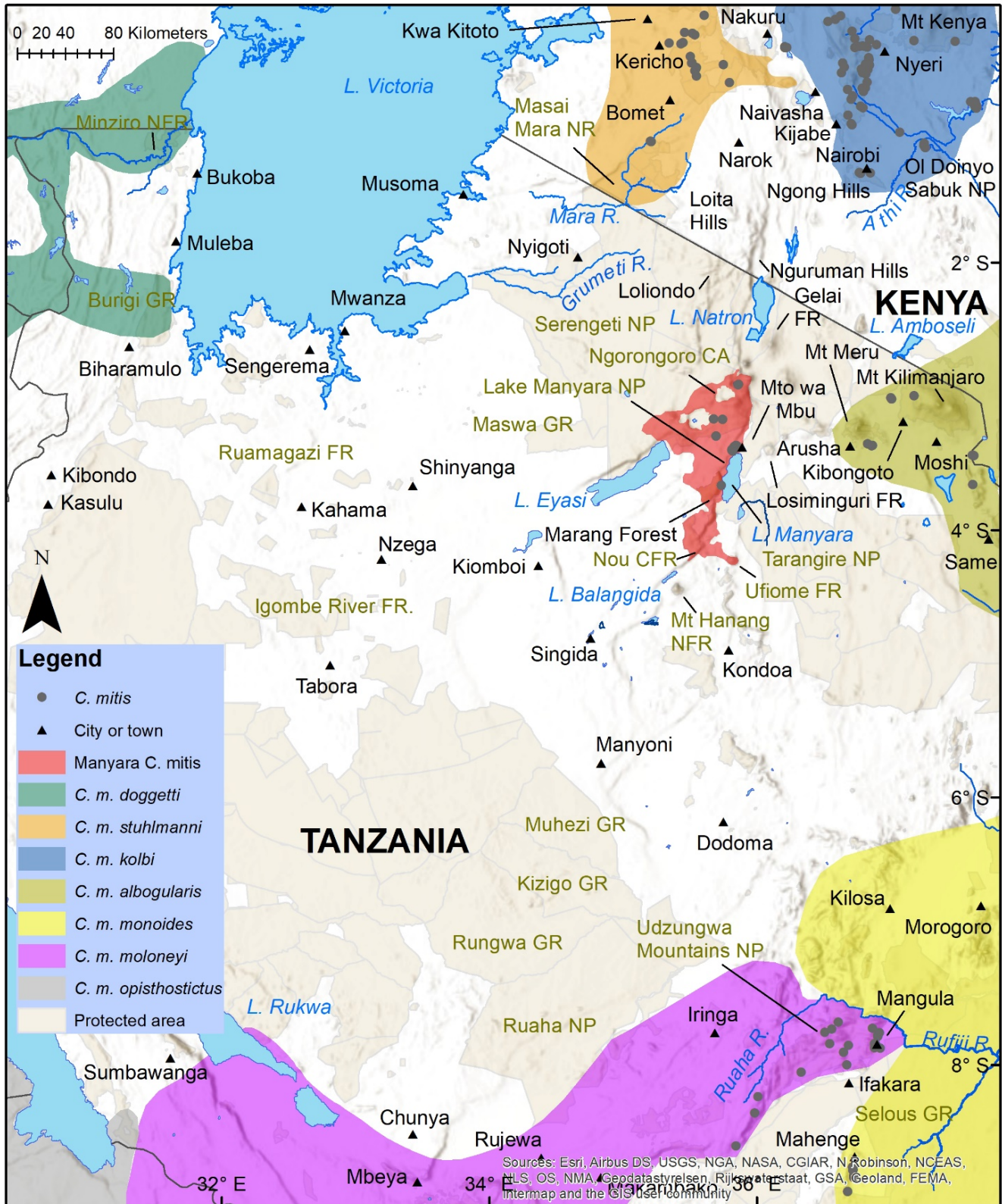


Figure 3. Approximate geographic distributions of the seven subspecies of gentle monkey *Cercopithecus mitis* in southwest Kenya, and northwest and central Tanzania. Some of the sites where the authors encountered *C. mitis* are indicated by grey circles.

Table 1. Taxonomic name, vernacular name, synonyms, type locality, geographic distribution (see maps in: Lawes *et al.* [2013] and De Jong and Butynski [2018]), and altitudinal limits in East Africa (i.e., Kenya, Tanzania, Uganda) for the eight subspecies of gentle monkey *Cercopithecus mitis* known to occur in Kenya and Tanzania (Figs. 1–3). Compiled from Pocock (1907), Elliot (1913), Allen (1939), Hill (1966), Kingdon (1971, 2013), Napier (1981), Groves (2001), Grubb (2001), Grubb *et al.* (2003), De Jong and Butynski (2012, 2018), Lawes *et al.* (2013), and Butynski and De Jong (2019a–f).

<p>Opisthostictus Section</p> <p><i>Cercopithecus mitis opisthostictus</i> Sclater, 1894 (not 1893 as sometimes cited). Mweru monkey</p> <p>Type locality: East shore of L. Mweru, extreme northeast Zambia.</p> <p>Synonyms: None</p> <p>Distribution: Large. Primarily southeast Congo Basin, DRC, and upper Zambezi Basin, Zambia. Limits poorly known. North limit near Lukuga R. and west bank Lualaba R. at c. 6°N, DRC. East limit L. Tanganyika, DRC, and Chambeshi R. and Lunsemfwa R., east Zambia. South limit c. 14°S, central Zambia. West limit perhaps Kasai R., southwest DRC, and upper Zambezi R., central east Angola and west Zambia. Approximate center of geographic distribution: Lubumbashi, extreme south DRC. Includes, as the only region in East Africa, the southeast littoral of L. Tanganyika, Tanzania (T. Davenport pers. comm. in Kingdon 2013).</p> <p>Altitudinal limits: 800–1,800 m asl.</p>
<p>Stuhlmanni Section</p> <p><i>Cercopithecus mitis stuhlmanni</i> Matschie, 1893 Stuhlmann’s blue monkey</p> <p>Synonyms: <i>carruthersi</i>, <i>elgonis</i>, <i>maesi</i>, <i>mauae</i>, <i>neumanni</i>, <i>otoleucus</i>, <i>princeps</i>, <i>schubotzi</i></p> <p>Type locality: Translation from German given in Moreau <i>et al.</i> (1946, p.403) as “North of Kinyawanga, north-west of Lake Albert, Congo Belge.” Corrected by Moreau <i>et al.</i> (1946, p.403) to, “North of Kinyawanga, near Beni, Semliki Valley, Congo Belge.” This site is north of L. Edward and west of the Rwenzori Mts., northeast Democratic Republic of Congo (DRC).</p> <p>Distribution: Large. Northeast DRC between Ubangi R. and Congo R. east of Itimbiri R, southwards east of Lualaba R. to about Lukuga R. Eastwards to southwest Kenya west of Eastern Rift Valley. Also, massifs of central north Uganda and southeast South Sudan. Approximate center of geographic distribution: Rwenzori Mts., southwest Uganda. Includes Semliki Forest, Budongo Forest, Kibale Forest, Maramagambo Forest, Kalinzu Forest, lower Bwindi Impenetrable Forest, Imatong Mts., Didinga Mts., Kidepo Valley, Mabira Forest, Mt. Elgon, Cherangani Hills, Kakamega Forest, Nandi Forest, and Mau Forest.</p> <p>Altitudinal limits: 1,600–3,800 m asl.</p>
<p><i>Cercopithecus mitis doggetti</i> Pocock, 1907 Doggett’s silver monkey</p> <p>Synonym: <i>sibatoi</i></p> <p>Type locality: Pocock (1907, p.691), “South-western Ankole, between Lakes Victoria and Albert Edward, Uganda.” Restricted by Moreau <i>et al.</i> (1946, p.402) to, “Between Lake Karengé and Burumba, north of Kagera River, S.W. Ankole, Uganda.”</p> <p>Distribution: Central east DRC, eastwards to extreme southwest Uganda, Rwanda, Burundi, and northwest Tanzania. Approximate center of geographic distribution: Lake Kivu, west Rwanda. Includes: upper Bwindi Impenetrable Forest, lower Virunga Volcanoes, Echuya Forest, Akagera NP, Sango Bay Forest, Manziro Forest, Busenya Forest, Nyungwe Forest, Kibira Forest, Rugege Forest, and Gombe Forest.</p> <p>Altitudinal limits: 770–2,700 m asl.</p>
<p>Albogularis Section</p> <p><i>Cercopithecus mitis kolbi</i> Neumann, 1902 Kolb’s monkey</p> <p>Synonyms: <i>hindei</i>, <i>nubilus</i></p> <p>Type locality: The type locality was unnecessarily “corrected” by Moreau <i>et al.</i> (1946). This “correction” is perpetuated by Hill (1966) and Napier (1981). Allen (1939) and Moreau <i>et al.</i> (1946) claim (p.402) that Neumann (1902) gave the type locality (as “Kedong Escarpment, east side of Mt. Kenya, Kenya Colony.” On this basis, they state (p.402), “The Kedong escarpment (often called “The Escarpment”), far from being east of Mount Kenya, is some seventy miles south-west of the mountain.” What Neumann (1902) states (p.144), however, is, “The type (No. 0.1.31) had been obtained by C. S. Betton on the Kedong Escarpment, Sept. 21, 1899. Two other males had been procured by A. H. Neumann at 8000–9000 feet, on the east side of Mt. Kenia, and by Lord Delamere in Roromo, British East Africa.” In short, Neumann does not claim that the Kedong Escarpment is “east of Mount Kenya”. As such, the type locality that he</p>

provides does not require correction.

The main railroad from Nairobi to Naivasha goes down the Kedong Escarpment through the Kijabe-Mai Mahiu region, central south Kenya. Kedong Escarpment is near the southwest edge of the geographic distribution of *C. m. kolbi*.

Distribution: Central Highlands of Kenya, east of Eastern (Gregory) Rift Valley. Approximate center of geographic distribution: Nanyuki, central Kenya. Includes: Meru Forest, Laikipia Plateau, Aberdare Range, Mt. Ol Doinyo Sabuk, Nairobi, and Ngong Hills. Not on Mt. Marsabit as sometimes stated (e.g., Astley Maberly 1960; Kingdon 1971; Williams 1981).

Altitudinal limits: 1,000–2,900 m asl.

Cercopithecus mitis albotorquatus de Pousargues, 1896
Pousargues' monkey

Synonyms: *phylax*, *rufotinctus*

Type locality: Unknown. East Africa (Rode 1938).

Distribution: Tana R. and coastal plains of north Kenya and extreme south Somalia. From Meru National Park (NP) eastwards along the Tana R. to the coast. North limit perhaps Caanoole R., Somalia. South limit about Kilifi Creek. Approximate center of geographic distribution: Tana River Primate National Reserve (NR), north coast of Kenya. Includes: Arabuko-Sokoke Forest, Mida Creek, Kilifi Forest, Boni-Dodori Forest, Lamu Archipelago, Witu Forest, Kipini Forest, Kora NP, Mwingi NR, and Meru NP.

Altitudinal limits: 0–300 m asl.

Cercopithecus mitis albogularis (Sykes, 1831)
Zanzibar Sykes' monkey

Synonyms: *kibonotensis*, *kima*, *maritima*

Type locality: Fixed by Schwarz (1927) as Zanzibar Island (now Unguja Island), c. 36 km off the north coast of Tanzania in the Indian Ocean.

Distribution: Southeast Kenya and northeast Tanzania from roughly Kilifi Creek along the Kenya coast southwards to about the Pangani R. and Zanzibar Island. Approximate center of geographic distribution: Mt. Kasigau, extreme southeast Kenya. Includes: Kibwezi Forests, Chyulu Hills, Mzima Springs, Kitobo Forest, Taita Hills, Mt. Kasigau, Shimba Hills, Tanga, North Pare Mts., South Pare Mts., East Usambara Mts., West Usambara Mts., Mt. Kilimanjaro, and Mt. Meru.

Altitudinal limits: 0–3,000 m asl.

Cercopithecus mitis monooides I. Geoffroy Saint-Hilaire, 1841
Tanzania Sykes' monkey

Synonym: *rufilatus*

Type locality: Unknown. East Africa (Rode 1938). Type locality of the synonym *C. m. rufilatus* Pocock 1907 given (p.702) as, “*Rufiji River, S. of Zanzibar.*” Type locality of adult male lectotype *monooides* selected by Schwarz (1928) is Rufiji R., 8°S, central coast east Tanzania. This is in or near the Rufiji R. Delta.

Distribution: Coastal plain of central and south Tanzania and extreme northeast Mozambique. From the Pangani R. southwards to Ruvuma R. Approximate center of geographic distribution: Rufiji R. Includes: Saadani NP, Wami R., Kilosa, Morogoro, Nguru Mts., Uluguru Mts., Selous GR, Kilombero Valley, Kichi Hills, Kilwa, Lindi, and Mafia Island.

Altitudinal limits: 0–2,590 m asl.

Cercopithecus mitis moloneyi Sclater, 1893
Moloney's white-collared monkey

Synonyms: None

Type locality: Near Karonga, north end of Lake Malawi, extreme north Malawi.

Distribution: From Udzungwa Mts., southwest Tanzania, southwards to the lower Kafue R. and middle Zambezi R., southeast Zambia, and Mt. Chitagal, northwest Mozambique. Approximate center of geographic distribution: North Luangwa NP, central east Zambia. Includes: Southern Highlands, L. Rukwa, Nyika Plateau, north shore L. Malawi, Mafinga Mts., Misuku Hills, Luangwa Valley, north Muchinga Mts., and Mt. Sanga.

Altitudinal limits: 500–2,600 m asl.



Figure 4. Ecoregions of southwest Kenya and northwest and central Tanzania (Olson *et al.* 2001), and the approximate geographic distribution of the six subspecies of gentle monkey *Cercopithecus mitis* nearest to the Manyara *C. mitis*.

numbers: 127793; 127794; 127795; 127796). It appears that these are the first specimens from the Manyara Population. As indicated in Table 2, 21 Manyara *C. mitis* specimens are known to be present in five museums. There may be specimens in other museums, particularly in Germany.

Summary of Published Records for the Manyara Population

1951 – Swynnerton and Hayman reported *C. mitis* at Mto wa Mbu (a town c. 300 m north of L. Manyara NP)

and refer to them as the “Kavirondo Blue Monkey” *Cercopithecus mitis neumanni* Matschie, 1906 (not 1905 as often cited). The type locality for *neumanni* is Kwa Kitoto, near Muhoroni, southwest Kenya, 48 km east of Kisumu (Moreau *et al.* 1946). Kwa Kitoto lies deep within the geographic distribution of *C. m. stuhlmanni*, c. 300 km north-northwest of the Manyara Population (Figs. 3 and 4). For the past 66 years, since Schwarz (1954), there has been wide agreement that *neumanni* is a synonym of *C. m. stuhlmanni*.

Table 2. Twenty-one Manyara *Cercopithecus mitis* specimens present in museums. The 10 specimens with an asterisk after the accession number were directly examined by the authors. Except for M-161108 and M-161109, all specimens collected near Lake Manyara at around 970 m asl (3,180 ft). Information presented here provided by specimen tags, collection curators, Napier (1981), Natural History Museum (2014), Trombone (2016), Grant and Ferguson (2019), and the authors.

Museum	Accession number	Nature of specimen	Locality	Age/sex	Date collected
Natural History Museum, London	ZD.1937.11.8.1*	Skin	North end L. Manyara	Adult female	1 May 1937
Natural History Museum, London	ZD.1951.371*	Skin, skull	Mto wa Mbu	Adult female	5 Sep 1948
Natural History Museum, London	ZD.1972.89*	Skin, skull, skeleton	Mto wa Mbu	Subadult female	13 Nov 1963
Natural History Museum, London	ZD.1972.90*	Skin, skull, skeleton	Mto wa Mbu	Adult male	13 Nov 1963
Natural History Museum, London	ZD.1972.91	Skull, Skeleton	Mto wa Mbu	Juvenile male	-
Royal College of Surgeons, London	RCS(OM) A74.62	Skull	North end L. Manyara	Adult female	1 Aug 1937
Royal College of Surgeons, London	RCS(OM) A74.63	Skull	L. Manyara	Adult female	-
Royal College of Surgeons, London	RCS(OM) G69.135	Skull	L. Manyara	Adult female	-
Royal College of Surgeons, London	RCS(OM) G82.141	Skull	L. Manyara	Male	-
Powell-Cotton Museum, Kent	NH.TAN.104	Skull, skin	Mto wa Mbu	Adult male	1 Apr 1939
Powell-Cotton Museum, Kent	NH.TAN.112	Skin	Mto wa Mbu	Juvenile female	Apr 1939
Field Museum of Natural History, Chicago	127793	Skin, skull, skeleton	Mto wa Mbu	Adult male	19 Sep 1928
Field Museum of Natural History, Chicago	127794	Skin, skull, skeleton	Mto wa Mbu	Adult female	19 Sep 1928
Field Museum of Natural History, Chicago	127795	Skin, skull, skeleton	Mto wa Mbu	Adult male	13 Nov 1928
Field Museum of Natural History, Chicago	127796	Skin, skull, skeleton	Mto wa Mbu	Adult female	13 Nov 1928
American Museum of Natural History, New York	M-161108*	Skin, skull	40 km east of Ngorongoro Crater	Adult male	28 Oct 1946
American Museum of Natural History, New York	M-161109*	Skin, skull	40 km east of Ngorongoro Crater	Adult male	29 Oct 1946
American Museum of Natural History, New York	M-161111*	Skin, skull	Mto wa Mbu	Adult male	25 Nov 1946
American Museum of Natural History, New York	M-161112*	Skin, skull	Mto wa Mbu	Adult male	25 Nov 1946
American Museum of Natural History, New York	M-161113*	Skin, skull	Mto wa Mbu	Subadult female	25 Nov 1946
American Museum of Natural History, New York	M-161114*	Skin, skull	Mto wa Mbu	Adult female	26 Nov 1946

1954 – Schwarz gave the southern limit of the geographic distribution of *stuhlmanni* as Mbulu, 96 km south of the Ngorongoro Crater and 27 km south of L. Manyara on the west rim of the Eastern Rift Valley (hereafter “ERV”). Mbulu is 820 km southeast of the type locality for *stuhlmanni* (i.e., Kinyawanga, Semliki Valley, northeast DRC). In the same publication, Schwarz identified the *C. mitis* at Mto wa Mbu as *kibonotensis* Lönnberg, 1908, claiming that this is the western-most site for *kibonotensis*.

1958 – Swynnerton listed *C. m. neumanni*, which he refers to (p.447) as “blue (Sykes’) monkey,” among the mammals of Ngorongoro Crater. See comments above concerning Swynnerton and Hayman (1951).

1966 – Hill (1966), following Schwarz (1954), referred the Manyara *C. mitis* to the Kilimanjaro blue monkey *C. a. kibonotensis*, and took Mto wa Mbu as the western-most population of *C. a. kibonotensis*. The type locality for *kibonotensis* is Kibongoto, southwest foothills of Mt. Kilimanjaro (c. 30 km northwest of Moshi), northeast Tanzania. Kibongoto is c. 130 km east of the Manyara Population. With the exception of Groves (2001, 2005) and Zinner *et al.* (2013a), all recent taxonomies treat *kibonotensis* as a synonym of *C. m. albogularis* (Grubb 2001; Grubb *et al.* 2003; De Jong and Butynski 2012, 2018; Kingdon 2013; Lawes *et al.* 2013; Butynski and De Jong 2019a, 2019b).

1968 – Booth observed and collected *C. mitis* both at Ngorongoro Crater and L. Manyara. She found that they did not match any described subspecies of *C. mitis*, the pelage coloration and pattern being distinct. Booth (1968, p.49) described the Manyara *C. mitis* as follows: “An average specimen (adult male from Mto wa Mbu, no. MYA 8) is a little browner than *stuhlmanni* but less so than *albogularis*. It has some speckling on the top of the head, unlike *stuhlmanni*, but less than in *albogularis*, so that there is a slight distinction between the speckled browband and the less speckled top of the head. It does not have the white half-collar as in *albogularis*, but the white of the throat is more extensive than in *stuhlmanni*. The length, direction, and ventral extent of the cheek fur are more like *albogularis* than *stuhlmanni*, but posteriorly this fur is continuous as in *stuhlmanni* with long speckled fur extending down each side of the neck to the shoulders. The ears have as much fur as the least heavily furred of *albogularis* specimens and might be intermediate between *stuhlmanni* and the somewhat more heavily furred *albogularis* likely to have been ancestral to it, judging from the length of the body fur. The underparts resemble *albogularis* rather than *stuhlmanni*.”

On this basis, she stated (p.49), “I interpret the *C. mitis* in this area as a hybrid swarm between *stuhlmanni* and *albogularis*. There is considerable individual variation, as might be expected in a hybrid swarm, but all specimens are intermediates between *stuhlmanni* and

albogularis.” To further support this view, she bred three *C. m. stuhlmanni* males with three *C. m. albogularis* females, and five *C. m. albogularis* males with five *C. m. stuhlmanni* females. These produced eight first-cross (F1) hybrids, the pelage of which she judged to be intermediate between *stuhlmanni* and *albogularis*. She concluded that these results (p.50) “strongly support the interpretation of the Ngorongoro and Lake Manyara population as a hybrid swarm.”

Booth (1968) stated that the *stuhlmanni* came from the Kenya Highlands west of the ERV and the “*albogularis*” from the Kenya Highlands east of the ERV. Note, however, that her treatment of *kolbi* as a synonym of *albogularis* is not recognized under today’s taxonomy. As such, all eight of her hybrids are now taken to be the product of *stuhlmanni* × *kolbi* parents, not *stuhlmanni* × *albogularis* parents. The type locality for *albogularis* is Zanzibar Island, Indian Ocean, east Tanzania, c. 460 km southeast of the Manyara Population, while the type locality for *kolbi* is in the vicinity of Kijabe, central south Kenya, c. 215 km north of the Manyara Population. Not only are these type localities c. 600 km apart, these two subspecies are phenotypically very different (Figs. 1 and 2; Napier 1981; De Jong and Butynski 2018).

It should also be noted that, apparently, none of the *stuhlmanni* × *kolbi* hybrids that Booth (1968) observed were adults. Of the four specimens at the Natural History Museum, London (= former British Museum of Natural History = BMNH), three are listed in Napier (1981) as juveniles (ZD.1972.92–ZS.1972.94) and one as an infant (ZD.1972.95). Based on their size, however, we judge ZD.1972.92–ZS.1972.94 to be subadults (i.e., 80–99% adult size) and ZD.1972.95 to be a large juvenile (i.e., 60–79% adult size; see below).

1970 – Rahm (1970) noted that Swynnerton and Hayman (1951) referred to the Manyara Population as *C. m. neumanni*, and that Booth (1968) referred to this population as a hybrid swarm intermediate between *C. m. stuhlmanni* and *C. m. albogularis*.

1971 – Kingdon (1971, p.241) stated the following as concerns the Manyara Population, “Intermediate animals, in which either bonnets or brow bands appear and showing a variety of mixed features are known from the rift wall above Lake Manyara.”

1981 – Napier (1981) agreed with Booth (1968), referring to the Manyara Population as a “hybrid swarm”, stating (p.97), “It appears that members of the *mitis* subspecies group from west of the Rift Valley interbreed with members of the *albogularis* group from the east at the northern end of Lake Manyara...”. She, however, argued that, based on their intermediate pelage characters, the parent subspecies are *C. m. doggetti* and *C. m. kibonotensis*, stating (p.97), “...in the Ngorongoro and Lake Manyara areas of Tanganyika, specimens showing characters intermediate between *C. mitis doggetti* and *C.*

mitis kibonotensis were collected at Mto wa Mbu at the northern end of Lake Manyara and presented to the Museum by Booth (BMNH 1972.89 and 1972.90). First cross hybrids bred in captivity at Tigon and showing similar intermediate characters were also presented to the Museum by Booth (BMNH 1972.92, 1972.93, 1972.94, 1972.95).” As mentioned above, *kibonotensis* is now a synonym of *albugularis* and the type locality for *doggetti* is between L. Kareng'e and Burumba, extreme southwest Uganda, c. 610 km west-northwest of L. Manyara.

After 1981 – Lernould (1988), Groves (1993, 2001, 2005), Grubb (2001, 2002), Detwiler *et al.* (2005), Davenport *et al.* (2013), Lawes *et al.* (2013), and Zinner *et al.* (2013a) all make brief mention of the Manyara Population, referring to it as either a hybrid swarm or comprising hybrids.

Study Areas

Field surveys specific to better understanding the taxonomic and conservation status of the Manyara Population were undertaken in two large study areas, one in central north Tanzania and one in southwest Kenya (Fig. 5). They were selected in order to provide a better understanding of the following for the Manyara Population: (1) coloration and pattern of the pelage and level of intra-population variation; (2) locations of the nearest other populations of *C. mitis*; (3) geographic distribution; and (4) conservation threats. In both study areas we focused research on the higher ground as that is where most of the forest is located in this, otherwise, semi-arid region. The exception was the ground-water forest of L. Manyara NP.

Lake Manyara Study Area

The Lake Manyara Study Area (c. 14,150 km²; 945–3,648 m asl) lies in central north Tanzania (Fig. 5) and includes Ngorongoro CA, L. Manyara NP, Nou CFR, and Mount Hanang Nature Forest Reserve (NFR). The limits of this study area are north 2.87°S, south 4.56°S, west 35.31°E, and east 35.98°E.

Ngorongoro CA (c. 8,280 km²; 1,030–3,648 m asl; Fig. 5) includes three large volcanic craters: Ngorongoro (c. 20 km wide; c. 260 km²; 2,200 m asl; the world's biggest unbroken caldera), Olmoti (c. 6.5 km wide; c. 30 km²; 3,050 m asl), and Empakaai (c. 6 km wide; c. 35 km²; 3,260 m asl). At 3,648 m asl, Mt. Loolmalasin is the third highest mountain in Tanzania. Mean annual rainfall varies across the area from c. 600 mm to c. 2,000 mm. The main vegetation types are montane forest, deciduous woodland, and Afromontane grassland/moorland. The upper limit of the montane forest is c. 3,260 m asl. Ngorongoro CA connects with the grasslands and *Acacia*-woodlands (>1,000 m asl) of Serengeti NP to the west, and with the plains of the Loliondo Game Control Reserve to the north. The south and east slopes comprise montane forest for which some of the more common trees are listed in

Appendix I. Fosbrooke (1972) presented a vegetation map for the Ngorongoro CA, together with estimates of coverage by the main vegetation types, as of about 1970. In 2000, there were 1,384 km² (17% cover) of forest, 1,427 km² of woodland (18% cover), and 177 km² (2% cover) of cultivated land in the Ngorongoro CA (Niboye 2010). The streams and rivers that drain southeast Ngorongoro CA connect with the groundwater forests of L. Manyara NP. Fosbrooke (1972) claimed that most of the water reaching L. Manyara from the Ngorongoro CA flows underground. The southeast boundary of Ngorongoro CA is near the west rim of the ERV at about 1,800 m asl, with L. Manyara NP to the southeast 15 km across unprotected land. This 15-km-wide area is largely composed of farmland where there is a high human density. The riparian forest that once connected Ngorongoro CA with L. Manyara NP no longer exists (AWF 2003; Google Earth 2019; T. Butynski and Y. de Jong pers. obs.).

Lake Manyara NP (680 km²; 945–2,040 m asl; Fig. 5), gazetted by UNESCO as a Biosphere Reserve in 1981, is located on the floor of the ERV. The dry land area is about 460 km². At 220 km², the alkaline L. Manyara covers about one-third of L. Manyara NP. The escarpment west of L. Manyara rises steeply to 1,300 m asl in the north and to 2,040 m asl in the south (Loth 1999). Mean annual rainfall varies across the area from c. 500 mm in the north to c. 1,200 mm in the south. The high water table and fertile soils support a high vegetative productivity and large mammal biomass. The main vegetation types to the north and west of the lake are riparian forest, gallery forest, *Acacia* ground water forest, *Acacia* ground-water woodland, thicket woodland, alkaline grassland, *Cynodon* grassland, and swamp. Forests cover c. 300 km² of the north, southwest, and west of the park. These forests are supported by several seasonal and perennial streams that run down the west wall of the ERV from the highlands, by perennial underground springs flowing through about 600 m of porous volcanic rock to the base of the ERV wall, by seasonal rivers from the east (e.g., Mauyuni R.) and, on the higher ground to the west, by adequate rainfall. Some of the more common trees in the vicinity of the lake and at the foot of the escarpment are listed in Appendix I. The edge of the groundwater forest on the lake-side is dominated by *Acacia xanthophloea* and *Phoenix reclinata*. The dominant grasses (Poaceae) here are *Cynodon dactylon* (L.) Pers. and *Cynodon plectostachyus* (K. Schum.) Pilg. (Greenway and Vesey-Fitzgerald 1969, 1972; Mwalyosi 1981; Loth and Prins 1986; Loth 1999; Roodt 2008; Kiffner *et al.* 2017; BirdLife 2019a; T. Butynski and Y. de Jong pers. obs.).

In 2009, Marang FR (250 km²; 1,200–2,040 m asl; Fig. 5) was added as a large southwest and west extension to L. Manyara NP, bringing the national park to its present size of 680 km². This dry, evergreen, montane forest is located on the west side of the ERV on the Mbulu Plateau. Some of the more common trees are listed in Appendix I.

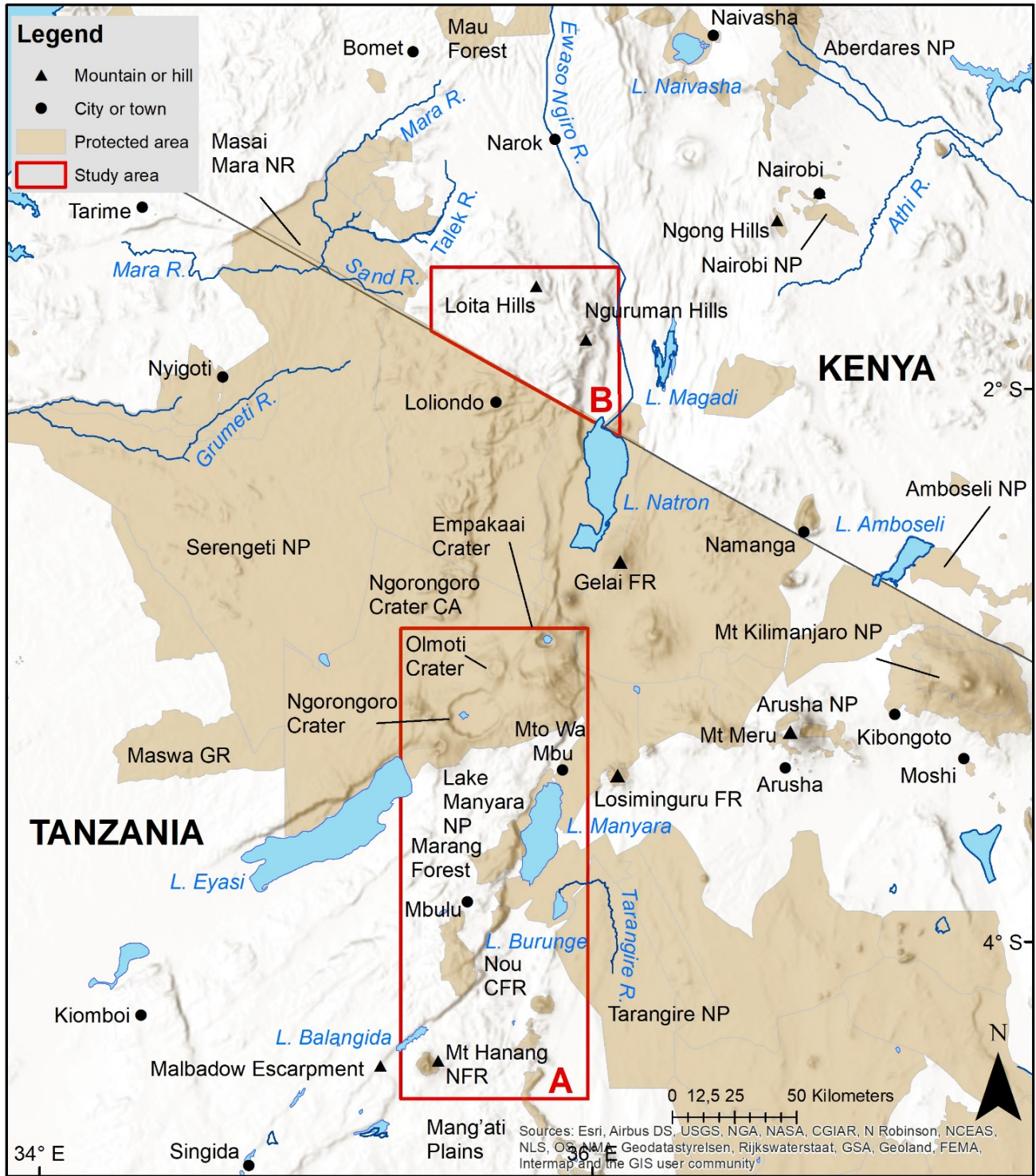


Figure 5. Lake Manyara Study Area (A) in central north Tanzania and Loita-Nguruman Hills Study Area (B) in southwest Kenya where gentle monkey *Cercopithecus mitis* surveys were undertaken during this study.

Nou CFR (320 km²; 1,800–2,416 m asl; Fig. 5) is located c. 13 km south of L. Manyara NP and covers the south end of the Mbulu Plateau. Most of Nou CFR lies above 2,150 m asl. Mean annual rainfall varies across the area from 700 mm to 1,200 mm (Kanyama and Kacheche 2016). A few of the more common species of tree in this montane forest are listed in Appendix I. Farm Africa (2019) gives the area of forest in Nou CFR as 320 km², but Google Earth (2019) indicates roughly 255 km² of forest.

Mt. Hanang NFR (= Gurue; 59 km²; 1,875–3,417 m asl; Fig. 5) lies c. 80 km south of L. Manyara NP. Mean annual rainfall varies with altitude from 750 mm to 2,000 mm (Krause and Böhme 2010). At 3,417 m asl, this extinct, isolated, volcano is Tanzania's fourth highest mountain. Mt. Hanang is surrounded by agriculture with a high human population. The many streams draining Mt. Hanang feed adjacent (saline) L. Balangida in the north and the surrounding plains. *Acacia* savanna covers most of the land below 1,700 m asl to the south (Mang'ati Plains) and east. The Malbadow Escarpment lies c. 25 km to the northwest. The main vegetation types on Mt. Hanang are deciduous bushland and cultivation (<1,800 m asl), grassland (1,800–2,000 m asl), montane forest (2,000–2,600 m asl), course grassland (2,600–2,700 m asl), and moorland (>2,700 m asl; Fuggles-Couchman 1953). The remaining forested area is c. 40 km² (Krause and Böhme 2010). Some of the more common tree species are listed in Appendix I.

Loita-Nguruman Study Area

The Loita Hills, southwest Kenya, lie east of Masai Mara NR and west of the contiguous Nguruman Hills (Fig. 5). The 50-km-long escarpment of the Nguruman Hills represents the west rim of the ERV. The south end of these hills reaches the Kenya-Tanzania border whereas the north end reaches the Loita Plains. Large areas of semi-arid, open, short-grass plains isolate the Loita Hills and Nguruman Hills from Mau Forest 80 km to the north, Ngong Hills 80 km to the northeast, and Ngorongoro Highlands (= Crater Highlands) 90 km to the south. In this study, the combined Loita Hills-Nguruman Hills area is referred to as the “Loita-Nguruman Study Area”. The limits of this study area (c. 3,530 km²; 610–2,680 m asl) are north 1.56°S, south 2.17°S, west 35.41°E, and east 36.10°E. Mean annual rainfall varies across the area from 400 mm to 1,200 mm. The streams of this area feed the Ewaso Ngiro R., Sand R., Telek R./Mara R., and L. Natron. The main vegetation types are dry montane forest, dry submontane forest, gallery forest, *A. xanthophloea* woodland, moist mixed woodland, mixed bushland, *Acacia* bushland, and short grassland. Grasslands cover much of the Loita Hills and are extensively used by livestock (Maundu *et al.* 2001; Karanja *et al.* 2002; Butynski and De Jong 2012). The area of forest is roughly 800 km². Some of the more common trees are listed in Appendix I.

Previous Research on *Cercopithecus mitis* by the Authors

We have considerable field experience with the taxonomy, biogeography, and ecology of *C. mitis*. We have made field observations (YDJ for 18 years; TMB for 41 years) in Kenya, Tanzania, Uganda, Rwanda, South Sudan, and DRC on eight of the currently recognized nine subspecies of *C. mitis* (*albogularis*, *albotorquatus*, *doggetti*, *kandti*, *kolbi*, *moloneyi*, *monoides*, *stuhlmanni*) in these six countries, and have reported the findings (e.g., Butynski 1999; Butynski and De Jong 2009, 2012, 2014, 2016, 2017, 2019a; De Jong 2012; De Jong and Butynski 2009, 2010b, 2010c, 2011, 2019). In addition, we are authors on the *C. mitis* “Category of Threat Assessments” for the *IUCN Red List* in 2008 (Kingdon *et al.* 2008) and 2016 (Butynski and De Jong 2019a), and for 12 *C. mitis* subspecies Degree of Threat Assessments in 2016, including seven of the eight subspecies known to occur in Kenya and Tanzania (Butynski and De Jong 2019b–h). We have observed >1,500 free-living *C. mitis* in >300 groups over much of the geographic distribution of this species in East Africa and photographed >700 individuals. A large selection of our photographs can be accessed on the “*Cercopithecus mitis* Photographic Map” at: <www.wildsolutions.nl/photomaps/mitis/> (De Jong and Butynski 2010b, 2019).

As a result of our extensive work on *C. mitis*, we have a good grasp of variations in the coloration and pattern of the pelage among *C. mitis* ssp. One consequence is that we became quickly aware of the significance of our initial observations on the Manyara *C. mitis* in October 2005.

Methods

Field surveys and free-living specimens

Specific to this study, we conducted four primate surveys, totalling 25 field days, in the two study areas (October 2005, November 2006, June 2009, July 2012). We drove about 2,025 km of transect in the study areas at an average speed of approximately 25 km/hr. Information collected during each vehicle census included date, weather conditions, start time, end time, places surveyed (GPS; Garmin GPSmap 60Cx), driving speed (GPS), and distance driven (GPS). Each encounter with primates was appointed a unique identification code. Information collected during each encounter included date, time, locality coordinates (GPS), altitude (GPS), tree density, vegetation type, species/subspecies, group size, and group composition. We gave particular attention to obtaining descriptions and photographs of adult males. Photographs were taken with a Nikon D70 digital camera fitted with a 400 mm Nikon lens, and with a Canon EOS 40D digital camera fitted with a Canon 75–300 mm lens.

The pelage coloration and pattern of adult males of all subspecies of *C. mitis* is darker, brighter, better

demarcated and, therefore, more distinctive than that of adult females or immature individuals. As such, in this study, only adult males were included in the analysis of pelage differences.

Transects tracks were saved by GPS and downloaded into a Dell Latitude notebook using Garmin MapSource and ESRI ArcMap software. The number of *C. mitis* groups encountered per kilometer and per hour were the indices used to assess relative abundance (Butynski and Koster 1994; White and Edwards 2000). Locations of all *C. mitis* groups were plotted on a map using ArcGIS (Version 10.7.1). All *C. mitis* locality records that we collected during other primate surveys in Kenya and Tanzania were added to the map. In ArcGIS, *C. mitis* groups with the same or similar phenotypes were joined in a polygon and overlaid with a vegetation map (FAO 2002; Figs. 3 and 4) to demarcate the approximate outer boundary of the geographic distribution of *C. mitis* subspecies in the region.

We contacted colleagues and searched websites to obtain additional photographs of Manyara *C. mitis*, particularly of adult males.

Museum surveys and museum specimens

To determine where Manyara *C. mitis* specimens are stored, we contacted mammal collection curators at major museums and searched mammal-collection on-line databases. This search yielded 21 Manyara *C. mitis* specimens at five museums (Table 2).

We directly examined 88 *C. mitis* specimen skins from East Africa, Zambia, and DRC; 45 at the Natural History Museum, London, 22 at The National Museums of Kenya, Nairobi, 15 at the Royal Museum for Central Africa, Tervuren, and 6 at the American Museum of Natural History, New York (Appendix II). These included Manyara *C. mitis* (n = 10), *C. m. kolbi* (n = 9), *C. m. albotorquatus* (n = 6), *C. m. albogularis* (n = 17), *C. m. monoides* (n = 4), *C. m. moloneyi* (n = 2), *C. m. stuhlmanni* (n = 15), *C. m. kandti* (n = 1), *C. m. doggetti* (n = 10), *C. m. opisthostictus* (n = 7), *C. m. opisthostictus* × *C. m. heymsansi* (n = 3), and captive bred *C. m. stuhlmanni* × *C. m. kolbi* hybrids (n = 4). Forty-five of these specimens are adult males.

For each specimen, information was collected from the specimen tag, descriptions of the pelage were made, and detailed photographs taken. Side-by-side comparisons were made among many of the specimens.

Describing hair and pelage coloration and pattern for *Cercopithecus mitis*

Many terms have been used to describe the complex coloration and patterns of the hair and pelage of cercopithecins. Some terms frequently used in the literature have several definitions, and the colors are often interpreted differently. This being the case, we strove to limit the number of terms and colors used for these descriptions. In particular, we adopted the word “flecked” over “agouti” and “grizzled”, both of which have multiple meanings, some of them strongly associated with the color grey.

Results

Geographic distribution of Manyara *Cercopithecus mitis*

A total of 24 groups of *C. mitis* were observed in the Lake Manyara Study Area and another five groups were heard but not observed. Of these 29 groups, 23 were in or near L. Manyara NP and six were in Ngorongoro CA (Figs. 3 and 5). These were probably unique groups in that almost all were encountered at distant sites along four widely-spaced transects. Seventeen of the encounters with groups occurred during vehicle censuses. The encounter rate with groups of *C. mitis* was several times higher in and near L. Manyara NP than in the Ngorongoro CA (Table 3). This monkey was most abundant in the ground water forests off the northwest corner of L. Manyara. A review of the literature presented no reports of *C. mitis* for Mt. Hanang NFR. During our 2-day survey at Mt. Hanang we did not encounter *C. mitis*, nor hear the “pyow” loud call. This call, typically given at least twice per day by group-living adult males (Butynski *et al.* 1992; Fuller and Cords 2017), can be heard by the human ear at >1 km (Brown 1989). Local farmers, police, and Forest Department rangers said that *C. mitis* does not occur on Mt. Hanang, nor in the vicinity. None of the colleagues questioned had seen or heard this species there (*C. Foley pers. comm.*; *A. Perkin pers. comm.*; *D. Peterson pers. comm.*; *J. Peterson pers. comm.*; *M. Peterson pers. comm.*; *S. Peterson pers. comm.*).

A review of the literature (e.g., Kingdon 1971; Broekhuis *et al.* 2018) revealed no records of *C. mitis* for the Loita-Nguruman Hills. We did not see or hear *C. mitis* in the Loita Hills during an 8-day survey (Butynski and De Jong 2012). None of the about 30 residents (including camp owners and safari guides) that we questioned claimed to have seen or heard *C. mitis* in the Loita-Nguruman Hills.

Table 3. Encounters during this study with groups of gentle monkey *Cercopithecus mitis* in the Lake Manyara Study Area, central north Tanzania, and Loita-Nguruman Study Area, southwest Kenya (Figs. 3 and 5).

Area	Number of groups encountered	Encounter rate during vehicle censuses	Altitude (m asl)
Lake Manyara NP	23	2.67 groups/hr; 0.16 groups/km (n = 16)	970–1,050
Ngorongoro CA	6	0.22 groups/hr; 0.02 groups/km (n = 1)	1,590–2,550
Mount Hanang NFR	0	0.00	-
Loita Hills	0	0.00	-

None of the researchers or naturalists familiar with the Loita-Nguruman Hills that we questioned were able to recall seeing or hearing *C. mitis* in the area (L. Bennun pers. comm.; S. Collins pers. comm.; B. Finch pers. comm.; S. Hatfield pers. comm.; R. Knocker pers. comm.; W. Knocker pers. comm.; Q. Luke pers. comm.; R. O'Meara; S. O'Meara pers. comm.).

Mt. Hanang and the Loita-Nguruman Hills have forest that appears highly suitable habitat for *C. mitis*. The apparent absence of this monkey at these two large sites, both within 50 km of at least one population of *C. mitis*, was unexpected.

Based on the above results, our other findings during field research on primates in East Africa, a review of the literature, and communications with naturalists and colleagues, it appears that the Manyara Population is geographically isolated from all other populations of *C. mitis* by unsuitable, semi-arid habitats; the nearest population of *C. m. albogularis* is c. 90 km east (Arusha NP, Mt. Meru, Tanzania) and the nearest population of *C. m. stuhlmanni* is c. 170 km northwest (Masai Mara NR, southwest Kenya (Figs. 3 and 4; Table 4).

Pelage characters of Manyara Cercopithecus mitis

The assessment of the pelage coloration and pattern of Manyara *C. mitis* is based on 14 free-living adult males (direct field observations and photographs) in the 24 groups we encountered, and on photographs taken by others of about 13 free-living adult males. These 27

“specimens” were obtained over an altitudinal range of 970–2,395 m asl.

With perhaps one exception, the coloration and pattern of the pelage of all 14 adult male Manyara *C. mitis* observed by us in the field looked the same. This was later confirmed by close examination of our photographs. The one possible exception was an adult male briefly observed on the east rim of Ngorongoro Crater (2,294 m asl). This individual may have had a slightly darker grey ventrum and was slightly more rufous around the base of the tail than the other 13 adult males observed by us. It should be noted, however, that these are perhaps the two parts of the body that vary the most in color in subspecies of *C. mitis* (T. Butynski and Y. de Jong pers. obs.). Examination of the photographs taken by others of about 13 other free-living adult males did not reveal individuals that differed in appearance from those that we observed.

In addition, we directly examined one adult male Manyara *C. mitis* specimen at the Natural History Museum and four adult male specimens at the American Museum of Natural History, and reviewed photographs of the two adult male specimens at the Field Museum of Natural History and the one adult male specimen at the Powell-Cotton Museum (Table 2). Variation in pelage color and pattern among these eight adult males was also found to be nearly absent.

We conclude that variation in pelage coloration and pattern among adult males in the Manyara Population is low. All of the 35 adult males assessed are distinct from adult males of all eight subspecies of *C. mitis* known

Table 4. Distance of Manyara *Cercopithecus mitis* from the nearest population of six other subspecies of gentle monkey *C. mitis*, and the altitudinal range and Ecoregion of the area that separates them (Figs. 3 and 4).

<i>Cercopithecus mitis</i> subspecies	Distance from Manyara <i>C. mitis</i> (km)	Direction from Manyara <i>C. mitis</i>	Altitudinal range of inter-lying area where <i>C. mitis</i> is absent (m asl)	Ecoregions of the inter-lying region where <i>C. mitis</i> is absent (Olson <i>et al.</i> 2001)
<i>C. m. albogularis</i>	90	East	1,250–1,900	Serengeti Volcanic Grasslands; East African Montane Forests (i.e., west Mt. Meru)
<i>C. m. stuhlmanni</i>	170	Northwest	1,500–1,900	Serengeti Volcanic Grasslands; Southern Acacia-Commiphora Bushlands and Thickets; East African Montane Forests (i.e., Loita-Nguruman Hills)
<i>C. m. kolbi</i>	190	North	1,400–1,900	East African Halophytics; Southern Acacia-Commiphora Bushlands and Thickets; Northern Acacia-Commiphora Bushlands and Thickets
<i>C. m. monoides</i>	260	Southeast	1,180–1,840	Southern Acacia-Commiphora Bushlands and Thickets; Central Zambebian Miombo Woodlands
<i>C. m. moloneyi</i>	330	South	900–1,840	Southern Acacia-Commiphora Bushlands and Thickets; Central Zambebian Miombo Woodlands; Itigi-Sumbu Thicket; Zambebian Flooded Grasslands
<i>C. m. doggetti</i>	465	Northwest	1,100–1,430	Serengeti Volcanic Grasslands; Southern Acacia-Commiphora Bushlands and Thickets; Central Zambebian Miombo Woodlands

for East Africa (Figs. 1 and 2; Table 5). In fact, as first pointed out by Booth (1968), the pelage of adult males in the Manyara Population is consistently intermediate between *albobularis* and *stuhlmanni* (but see below).

Appendix III presents a visual comparison of the pelage coloration and pattern of the six Manyara *C. mitis* specimens at the American Museum of Natural History. Note the low level of inter-individual variation.

The pelage of adult female Manyara *C. mitis* (Fig. 6) is also distinct from the pelage of adult females of the eight subspecies of *C. mitis* known for East Africa and intermediate between *albobularis* and *stuhlmanni*. This too is in agreement with the observations of Booth (1968).

Given the isolation and the distinctive and consistent coloration and pattern of the pelage of Manyara *C. mitis*, it is representative of a new subspecies and requires formal classification. Here we designate this new subspecies.

Body size and shape, and pelage coloration and pattern of Manyara *C. mitis* resemble a typical adult member of the *Cercopithecus mitis/albobularis* Subgroup (Kingdon 1997, 2013, 2015; Grubb *et al.* 2003; Lawes *et al.* 2013) with general characters of *C. mitis* as presented by Hill (1966); moderately large arboreal monkey with long-tail and black arms, hands, feet, and distal half of tail; whiskers with heavily annulated hairs that are directed backwards and/or downwards, forming a neat, smooth, ovoid pad; ventrum pale grey to black; no beard.

The Manyara Monkey

Family Cercopithecidae Gray, 1821
Genus *Cercopithecus* Linnaeus, 1758
Species *Cercopithecus mitis* Wolf, 1822

Cercopithecus mitis manyaraensis, ssp. nov.

Holotype. ZD.1937.11.8.1; adult female (Fig. 7). Skin (only) at the Natural History Museum, London, United Kingdom. The original specimen tag gives the collector as B. Cooper. A second specimen tag gives Sir F. Colyer as an additional collector. The original specimen tag gives the collection date as 1 May 1937 but Napier (1981, p.111) and Natural History Museum (2014) give the collection date as 1 August 1937. The original specimen tag identifies this specimen as *Cercopithecus leucampyx kibonotensis*. It was identified as “*Cercopithecus leucampyx neumanni*?” by Napier (1981, p.111). A third specimen tag identifies this specimen as *doggetti* × *kibonotensis*.

Type locality. North end of Lake Manyara, Mbulu District, Northern Region, central north Tanzania. 3°22'S; 35°50'E; 970 m asl (3,180 ft asl).

Paratopotype 1. ZD.1972.90; adult male (Fig. 8). Skin, skull, and skeleton at the Natural History Museum, London, United Kingdom. Both hands and both feet missing from the skin. Face and brow-band damaged. Collected by Cynthia P. Booth on 13 November 1963 and identified by her as “*Cercopithecus mitis ?stuhlmanni X*”.

Paratopotype 1 locality. Mto wa Mbu, north end of Lake Manyara, Mbulu District, Northern Region, central north Tanzania. 3°22'S; 35°50'E; 976 m asl (3,200 ft asl).

Paratopotype 1 body measurements. Taken from the original specimen tag: length of head + body: 606 mm; length of tail: 805 mm; length of foot: 165 mm; length of hand: 114; length of ear: 37 mm; body weight: 7,930 grams.

Paratopotype 2. Live adult male in the photographs in Figure 9. This adult male also presented in photographs 4a and 4b in Figure 2. All photographs taken 15 June 2009 by Yvonne de Jong and Thomas Butynski.

Paratopotype 2 locality. Ground water forest at north end of Lake Manyara National Park near Mto wa Mbu, Mbulu District, Northern Region, central north Tanzania. 3°22'40"S, 35°49'55"E; 970 m asl (3,180 ft asl).

Hypodigm. Table 2 lists the 21 specimens known to be present in museums, 16 of which are represented by skins. Photographs of all 16 skins available at: <www.wildsolutions.nl/manyaraensis>. Photographs of free-living individuals available on the “*Cercopithecus mitis* Photographic Map” at: <www.wildsolutions.nl/photomaps/mitis/>, and at <iNaturalist.com>. See also Appendix III.

Description of holotype. Adult female. Body measurements and color of iris as written on original specimen tag: length of head + body: 440 mm; length of tail: 670 mm; length of foot: 129 mm; length of ear: 34 mm; iris: light brown. Muzzle and around mouth with sparse cover of pale grey hairs. Cheek whiskers full, hairs of medium length (30–35 mm), projecting backwards and slightly downwards covering upper neck and front of shoulders. Cheek whiskers and hairs of brow-band heavily flecked grey, black, and yellowish-buff (nearly same color as back), contrasting with black crown and nape. Demarcation between brow-band/whiskers and crown/nape distinct but diffuse. Brow-band with hairs of medium length (16 mm), black over basal half, projecting forwards and upwards. Crown and nape black with some yellowish-buff flecking; flecking densest at front and center of crown. Hairs of crown tipped black, middle with one 3-mm-wide yellowish-buff band, base blackish. Hairs

Table 5. Pelage characters of adult male *Manyara Cercopithecus mitis* compared with adult males of the geographically nearest four subspecies: *C. m. albogularis*, *C. m. kolbi*, *C. m. stuhlmanni*, *C. m. doggetti*. Based on the literature, museum specimens, photographs, and authors' field observations (Figs. 1 and 2). An asterisk designates those five traits most useful for distinguishing *Manyara Cercopithecus mitis* from the other four taxa.

Section	Albogularis Section		Manyara <i>C. mitis</i>	Stuhlmanni Section	
	<i>C. m. albogularis</i>	<i>C. m. kolbi</i>		<i>C. m. stuhlmanni</i>	<i>C. m. doggetti</i>
Subspecies/body part					
Within subspecies pelage coloration and pattern variation	Very high.	Medium.	Low.	High.	High.
Number of synonyms	3	2	0	8	1
Brow-band sharply demarcated*	No.	No.	Yes.	Yes.	Yes.
Color of brow-band and whiskers	Flecked yellowish-buff and grey or olive and grey. Not same color as back.	Flecked dark grey and olive-yellow or olive-buff. Not same color as back.	Flecked grey, black, and yellowish-buff or olive. Nearly same color as back. Basal half of hairs of brow-band sometimes black.	Flecked off-white, grey and black. Nearly same color as back.	Olive-grey flecked black. Nearly same color as back.
Crown*	Flecked olive and grey with yellowish-rufous wash.	Flecked olive and dark grey with rufous wash.	Black with cream-buff flecking. Flecking densest at front and center of crown.	Jet black. Small patch of flecked reddish-yellow and black hairs sometimes visible at center of crown.	Jet black. Small patch of flecked reddish-yellow and black hairs sometimes visible at center of crown.
Color contrast between brow-band/whiskers and crown/nape*	Slight.	Slight.	Moderate.	High.	Very high.
Demarcation between brow-band/whiskers and crown/nape*	Slight.	Slight.	Not sharp (i.e., blurred).	Sharp.	Very sharp.
Ear hair fringe	Medium or long. Thinly haired. White, off-white, or pale grey.	Long. Densely haired. Covers ears. White, off-white, or cream.	Medium. Whitish, pale grey, or pale cream.	Varies from absent to medium, and from thinly haired to ample. White or buff.	Very short and thinly haired. Whitish or pale grey.
Iris	Amber.	Amber.	Light brown.	Muddy brown.	Muddy brown.
Throat	White.	Bright white.	White or whitish.	Whitish or pale grey.	Whitish or pale grey.
Neck-collar (% complete)*	White or off-white. Diffuse. Narrow. (60%).	Bright white. Hair long and dense, forming a sharply demarcated, broad, ruff. (90%).	Light grey flecked black. Diffuse. (70%).	Absent. (0%).	Absent. (0%).
Black shoulder-band	Absent.	Absent.	Narrow and diffuse. Flecked grey.	Narrow.	Width variable.
Back	Flecked grey and olive with rufous wash.	Flecked grey and olive with rufous to chestnut wash.	Silver-grey heavily flecked black with olive or yellow wash.	Flecked grey and black.	Light silver-grey flecked olive with yellowish-brown wash.
Rump	Flecked grey and olive with strong orange-yellow or reddish-yellow wash.	Flecked grey and olive with strong orange-yellow or chestnut wash.	Silver-grey heavily flecked black with reddish-olive or yellowish-olive wash.	Flecked grey and black.	Light silver-grey flecked olive with yellowish-brown wash.
Outer arms	Shiny black.	Black.	Black.	Jet black.	Jet black.
Outer thighs	Blackish or flecked black and grey, or grey lightly flecked black.	Grey flecked black.	Grey heavily flecked black or dark grey.	Black or blackish flecked grey.	Black or blackish lightly flecked grey.
Outer lower legs	Blackish or heavily flecked blackish and grey, or grey lightly flecked black.	Grey flecked black.	Dark grey flecked black becoming less flecked towards ankle.	Black or blackish flecked grey.	Black or blackish lightly flecked grey.
Color contrast between ankles and black dorsum of feet	Moderate.	Moderate to high.	Moderate to high.	Low to none.	Low to none.
Dark grey or black chest-band	Absent.	Absent.	Narrow. Complete or incomplete.	Complete but diffuse towards center.	Complete but diffuse towards center.
Center of ventrum	Greyish or off-white.	Grey or dark grey.	Pale grey to dark grey. Flecked grey or black.	Grey to blackish, sometimes dark grey flecked black.	Pale grey.



Figure 6. Three adult female Manyara *Cercopithecus mitis*, Mto wa Mbu, north end of Lake Manyara National Park, central north Tanzania. Photographs by Yvonne de Jong and Tom Butynski.



Figure 7. Holotype *Cercopithecus mitis manyaraensis*, ssp. nov. (ZD.1937.11.8.1). Adult female. Courtesy of the Trustees of the Natural History Museum, London. Photographs by Yvonne de Jong and Tom Butynski.



Figure 8. Paratype 1. *Cercopithecus mitis manyaraensis*, ssp. nov. (ZD.1972.90). Adult male. Courtesy of the Trustees of the Natural History Museum, London. Photographs by Yvonne de Jong and Tom Butynski.



Figure 9. Paratopotype 2 *Cercopithecus mitis manyaraensis*, ssp. nov. Live adult male in these five photographs. Mto wa Mbu, Lake Manyara National Park, central north Tanzania. Photographs by Yvonne de Jong and Tom Butynski.

of nape 45 mm long, tip black, two yellowish-buff bands, base dark grey. Hairs of ear fringe medium length (12 mm), whitish. Front of ears nearly naked. Hairs of back of ears short, blackish. Chin whitish. Neck-collar distinct but diffuse, light grey flecked black, *c.* 70% complete, being absent from nape. Ends of neck-collar terminate *c.* 80 mm apart near nape. Shoulder-band black, flecked grey, complete, narrow, distinct but diffuse. Back silver-grey, heavily flecked black with faint olive wash. Base of hairs at mid-back dark grey. Flanks similar to back but greyer. Rump with rufous wash becoming increasingly intense towards tail and around the proximal *c.* 5% of tail. Sides of base of tail, under base of tail, and around callosities and anus, with rufous hairs (not flecked) 30–40 mm long. Outer and inner arms and hands black. Outer thighs grey, heavily flecked dark grey and black. Back of thighs pale grey. Outer lower legs dark grey, flecked black becoming less flecked towards ankles. Sharp demarcation and moderate to high contrast between grey ankles and black feet. Inner legs dirty white proximally becoming blackish distally. Hairs of throat pale yellow tipped blackish. Chest-band distinct, black, narrow, complete but diffuse at center. Nipples long. Ventrums dark grey, flecked blackish; proximal half of hairs light grey and distal half with four blackish bands. Proximal *c.* 65% of tail black, heavily flecked grey, becoming less flecked distally. Distal *c.* 35% of tail black with light flecking. Ischial callosities bare, dark grey, partly hidden under fur of upper legs.

Diagnosis. One hundred percent diagnosable from all other currently recognized taxa in the *Cercopithecus (nictitans)* Superspecies when the following suite of pelage characters is applied. Crown and nape black with yellowish-buff flecking that is densest at front and center of crown. Brow-band distinct from crown; obvious contrast in color between brow-band/whiskers and crown, but demarcation not sharp. Brow-band hairs black over basal half in some individuals. Neck-collar diffuse, light grey, flecked black, about 65–75% complete, not reaching nape. Band across shoulders black, flecked grey, narrow, diffuse. Chest-band narrow, black, diffuse at center (Table 5).

Sexual dimorphism. Adult male (Table 5) and adult female similar, but pelage slightly darker and pelage pattern more sharply demarcated in adult male. Adult male typically with slightly more rufous on back, rump, and around base of tail than adult female. Scrotum bare, skin dark grey. Adult male noticeably larger than adult female; adult female estimated to weigh 60% as much as adult male.

Body size. Means and ranges for five standard field body measurements from five adult males and two adult females are presented in Table 6. The raw data are given in Appendix IV. These values are similar to those for other subspecies of *Cercopithecus mitis* (Lawes *et al.* 2013, p.362).

Variation. Intra-subspecific variation in coloration and pattern of the pelage of adults observed in the field, in photographs, and in museum collections is low relative to adults of several other subspecies of *C. mitis* (e.g., *albogularis*, *albotorquatus*, *doggetti*, *kanti*; see below). No evidence of clinal variation in pelage among adults. Pelage of individuals in south L. Manyara NP (980 m asl) similar to that of adults 38 km to the north at Mto wa Mbu (970 m asl) and 85 km to the north in Ngorongoro CA (2,294 m asl). One adult male on the east rim of Ngorongoro Crater (2,294 m asl) may have had slightly darker grey ventrum and slightly more intense rufous around the base of the tail.

Geographic distribution. Endemic to the Lake Manyara-Ngorongoro Region. Allopatric in central north Tanzania on the floor, west escarpment, and rim of the Eastern (Gregory) Rift Valley to the northwest, north, south, and west of L. Manyara (Fig. 10). Known altitudinal limits are *c.* 960 m asl (3,150 ft asl; L. Manyara) and *c.* 2,550 m asl (8,366 ft asl; east rim of Empakaai Crater). It is likely, however, that the upper altitudinal limit is congruent with that of forest in the Ngorongoro CA at about 3,260 m asl (10,700 ft asl). Limits of the known geographic distribution are north 2.911°S; south 4.262°S; east 35.934°E; west 35.515°E. This yields a known geographic distribution of *c.* 1,480 km². Limits of the probable geographic distribution, based on presence of

Table 6. Means and ranges for five standard field body measurements from five adult male and two adult female Manyara monkeys *Cercopithecus mitis manyaraensis*. The raw data for these seven specimens are presented in Appendix IV.

Sex	Male			Female		
	Mean	Range	N	Mean	Range	N
Head-body length (mm)	538.6	482–606	5	456.5	440–473	2
Tail length (mm)	752.0	690–805	5	682.0	670–694	2
Hindfoot length (mm)	161.6	154–170	5	133.0	129–137	2
Ear length (mm)	37.0	-	1	34.0	-	1
Weight (kg)	7.6	7.0–7.9	3	-	-	-

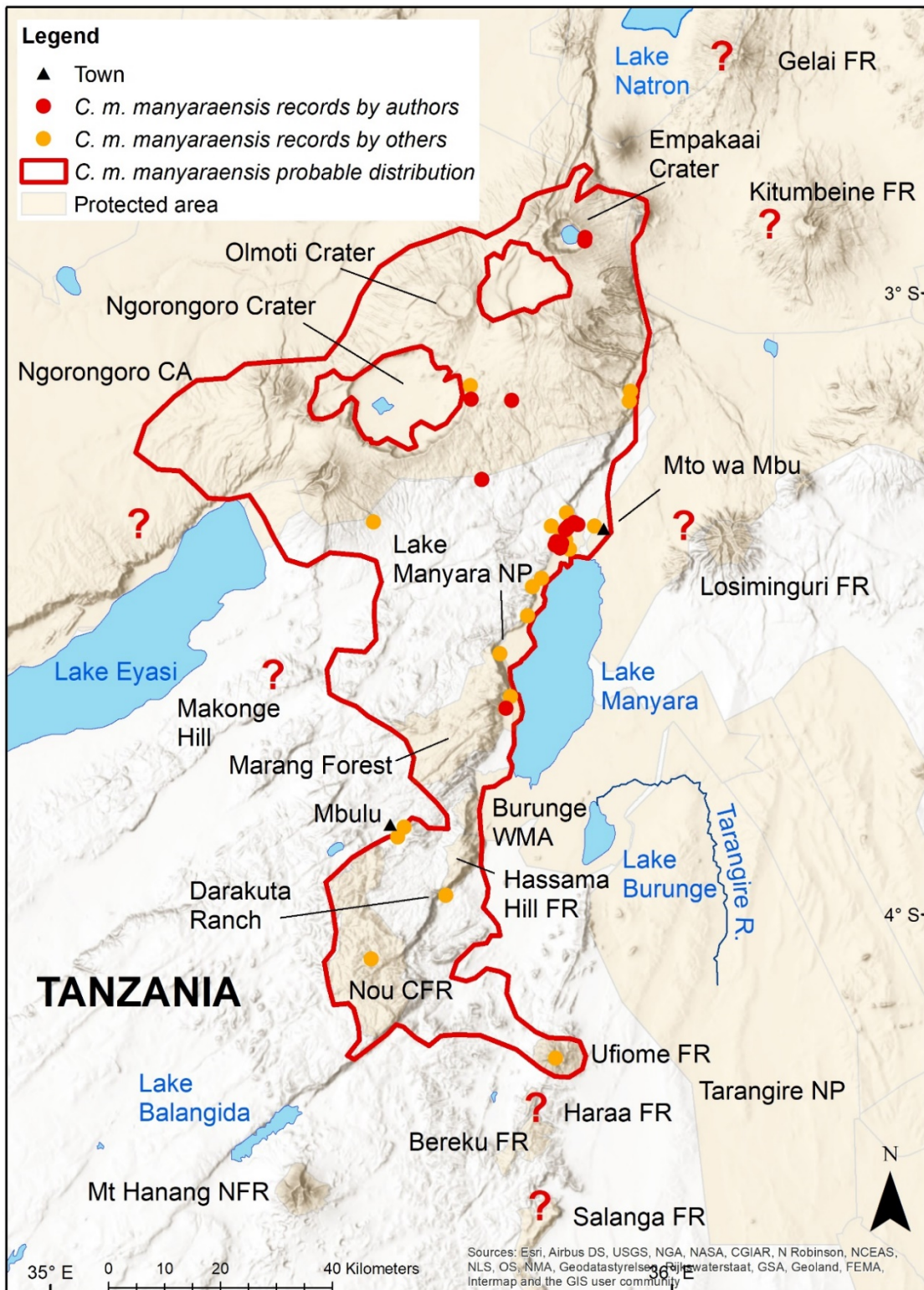


Figure 10. Red polygon depicts the probable geographic distribution of Manyara monkey *Cercopithecus mitis manyaraensis*, ssp. nov., based on locality records (dots) and availability of suitable habitat. Type locality is Mto wa Mbu. Sources of these data are Schwarz (1954), Hill (1966), Napier (1981), iNaturalist (2019), C. Foley (pers. comm.), and Y. de Jong and T. Butynski (pers. obs.). A red '?' demarcates an area in need of a ground survey to determine presence/absence of *C. mitis*.

suitable habitat (i.e., forest), are north 2.80°S; south 4.26°S; east 35.96°E; west 35.14°E. This gives a probable geographic distribution of roughly 5,865 km² (including c. 2,055 km² of protected forest). The known geographic distribution includes parts of Ngorongoro CA, L. Manyara NP (including Marang Forest), Dakakuta Ranch, Nou CFR, and Ufiome FR. Given that the area of forest within the probable geographic distribution of this forest-dependent subspecies is about 2,055 km², the “Area of Occupancy” (IUCN 2012) cannot be much larger than 2,055 km². The geographic barrier isolating *manyaraensis* from other *C. mitis* populations is the surrounding semi-arid, non-forest habitats through which there are no perennial rivers and the forest corridors they often support.

Cercopithecus m. manyaraensis is absent from several large forests in southwest Kenya and northwest Tanzania (Figs. 3, 4, 5 and 10), all of which have habitat that appears suitable. Most unexpected is its absence from the Loita-Nguruman Hills (Kingdon 1971; Butynski and De Jong 2012; Broekhuis *et al.* 2018; L. Bennun pers. comm.; S. Collins pers. comm.; B. Finch pers. comm.; S. Hatfield; R. Knocker pers. comm.; W. Knocker pers. comm.; Q. Luke pers. comm.; R. O’Meara pers. comm.; S. O’Meara pers. comm.), particularly given that the, often sympatric, Mau forest guereza *Colobus guereza matschiei* Neumann, 1899 is common here. *Cercopithecus m. manyaraensis* is apparently also absent from the region between Loita-Nguruman Hills and Ngorongoro CA (including the Gelai, Waso, Olaihiri, Soit or’gos, Soit Sambu, Magaiduru, and Loliondo areas [Kingdon 1971; M. Borner pers. comm.; C. Foley pers. comm.; R. Knocker pers. comm.; S. Peterson pers. comm.; D. Rentsch pers. comm.]), as well as from Mt. Hanang (Kingdon 1971; C. Foley pers. comm.; A. Perkin pers. comm.; D. Peterson pers. comm.; J. Peterson pers. comm.; M. Peterson pers. comm.; S. Peterson pers. comm.; this study). Although these sites are located 15–90 km from the known geographic distribution of *manyaraensis*, the inter-lying area is semi-arid.

Ecology and behaviour. *Cercopithecus m. manyaraensis* has never been the focus of a behavioral ecology field study and, therefore, it remains poorly known. This subspecies lives in forest. Habitats include *Acacia* ground water woodland, *Acacia* ground water forest, and riparian forest on the floor of the ERV at L. Manyara, and gallery forest, mid-altitude forest and montane forest on the escarpment of the ERV and over the Mbulu Plateau and Ngorongoro Highlands. In addition, *manyaraensis* uses areas close to humans, including hotels, safari camps, farms, and settlements. See Appendix I for lists of some of the more common species of trees where *manyaraensis* occurs.

Mean annual rainfall over both the known and probable geographic distributions ranges from 500 mm at

the north end of L. Manyara to 1,200 mm along the escarpment of the ERV and at Ngorongoro Crater.

Although mainly arboreal, *C. m. manyaraensis* regularly goes to the ground to rest, travel, and forage. During this study, *manyaraensis* was often observed feeding on the ripe fruit of *Ficus sycomorus* and *Ficus natalensis*. Other tree species used include *Ficus thonningii*, *Trichilia emetica*, *Acacia tortilis*, *Rauwolfia caffra*, *Kigelia africana*, and *Sterculia africana*.

Etymology. The name “*manyaraensis*” acknowledges Lake Manyara, Tanzania, the type locality.

Vernacular name. Manyara monkey.

Discussion

Characters distinguishing Cercopithecus mitis manyaraensis from the four geographically nearest subspecies

The most useful characters of the pelage for distinguishing *C. m. manyaraensis* from the four subspecies of *C. mitis* that are geographically closest relate to the brow-band, crown, hairs on fringe of ears, neck-collar, shoulder-band, chest-band, and overall amount of brown/rufous in the pelage:

Cercopithecus m. albogularis and *C. m. kolbi*, both in the Albogularis Section, differ from *manyaraensis* (as well as from *stuhmanni* and *doggetti*) in that there is little or no demarcation between brow-band and crown, crown not black, white/cream hairs on fringe of ears long, neck-collar white and well demarcated, black shoulder-band absent, black chest-band absent, dark grey ankles, and considerable buff, brown, and/or reddish flecking (varying from yellowish-buff to chestnut) in the pelage of the head, neck, shoulders, back, rump, base of tail, and around ischial callosities (Table 5).

Cercopithecus m. stuhmanni and *C. m. doggetti*, both in the Stuhmanni Section, differ from *manyaraensis* (as well as from *albogularis* and *kolbi*) in that the crown is jet black (although a small patch of flecked reddish-yellow and black hairs sometimes visible at center of crown) and sharply demarcated from the brow-band, white/whitish hairs on fringe of ears short or absent, white neck-collar absent, black shoulder-band present, black chest-band present, blackish or black ankles, and almost no buff, brown, or reddish in the pelage, being limited, if present, to the crown (where it is typically concealed under black hair), base of tail, and around ischial callosities (Table 5).

With two exceptions, the coloration and pattern of the pelage of *C. m. manyaraensis* is intermediate between *C. m. albogularis/kolbi* and *C. m. stuhlmanni/doggetti* (Table 5). In some *manyaraensis* the proximal c. 50% of the hairs of the brow-band is black. With these hairs directed upwards, the effect is that of a second, lower, brow-band. We refer to this as the “black sub-brow-band.” The other trait where *manyaraensis* appears to not always be intermediate is the sharp demarcation and high contrast of the grey ankles against the black feet in some individuals. In *Cercopithecus (nictitans)*, these two characters are also present in at least some *C. m. opisthostictus* (Figs. 1, 2 and 11).

Pelage of Cercopithecus mitis manyaraensis is intermediate

Our findings agree with Booth’s (1968) observation that individuals in the Manyara Population are phenotypically intermediate between *stuhlmanni* and *albogularis* (the two geographically nearest subspecies from either side of the ERV) as concerns pelage coloration and pattern. Our study also found, however, that the pelage of *manyaraensis* is likely intermediate between all other possible Stuhlmanni Section \times Albogularis Section subspecies combinations for the East African subspecies (e.g., *doggetti* \times *albogularis*, *doggetti* \times *kolbi*, *doggetti* \times *monoides*, *stuhlmanni* \times *albotorquatus*, *stuhlmanni* \times *monoides*).

Pelage variation within Cercopithecus mitis manyaraensis is low

Booth (1968) visited the Manyara Population to make field observations and collect specimens. Based on this research, she stated (p.50), “The specimens in the Ngorongoro and Lake Manyara area of Tanganyika were provisionally interpreted as a hybrid swarm between *albogularis* and *stuhlmanni* on account of their intermediate characteristics and individual variability.” As indicated above, this interpretation of the Manyara Population by Booth has been widely cited.

We did not find the “considerable individual variation” that Booth claims (p.49). Booth gives no information on the number and age/sex of the individuals she observed and collected, nor details on the nature and degree of the individual variation that she saw. We suspect that the numbers of individuals observed and collected by Booth in the Manyara Population were small. Of the specimens collected, two immature individuals and one adult male (paratopotype 1) are in the Natural History Museum, London. As there are no *manyaraensis* specimens in The National Museum of Kenya, Nairobi, we suspect that the total number of specimens collected by Booth was three. Booth gives no indication that she examined museum specimens of *manyaraensis* beyond those that she collected. It is likely that Booth’s incorrect

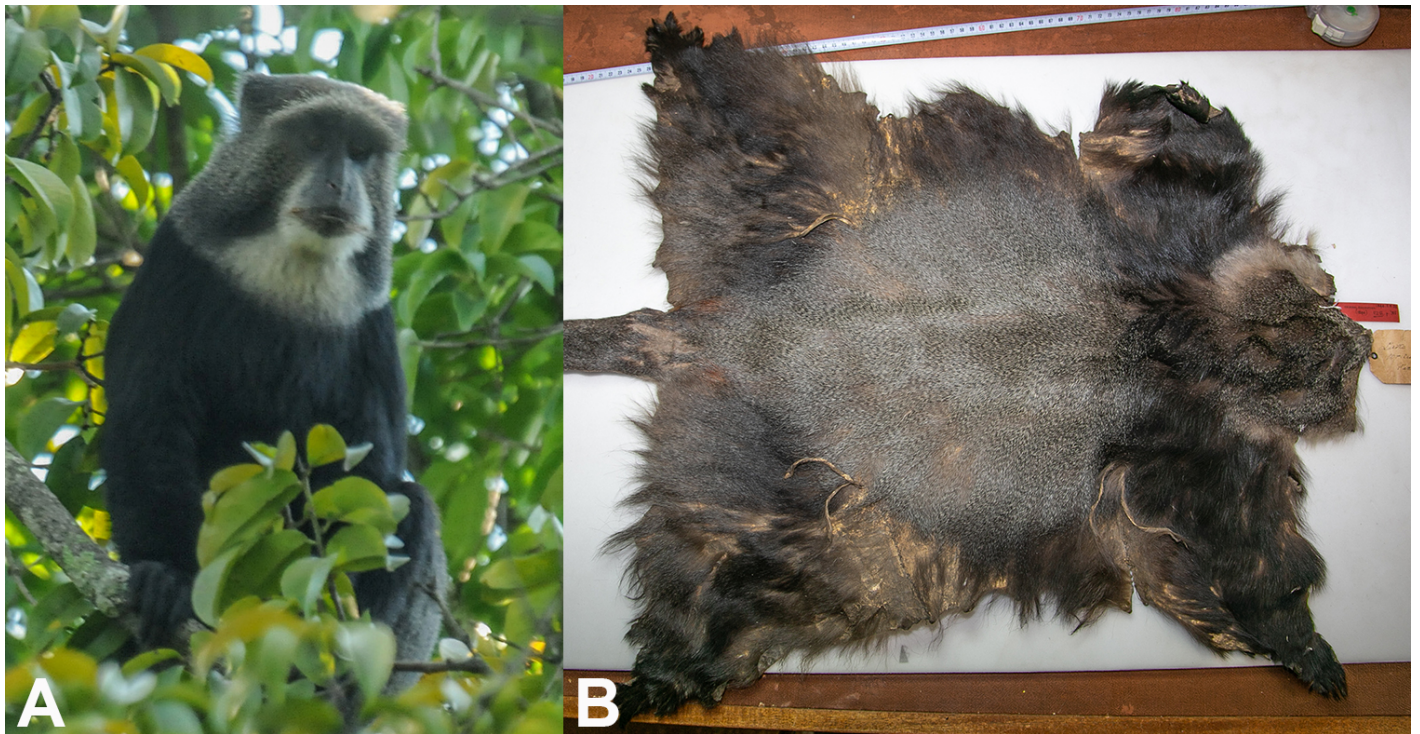


Figure 11. Mweru monkey *Cercopithecus mitis opisthostictus*. A. Adult male, Imande, northeast Zambia (photograph by Nick Hart); B. Adult male, east shore of Lake Mweru, northeast Zambia (ZD.1894.3.8.22, lectotype). Courtesy of the Trustees of the Natural History Museum, London. Photograph by Yvonne de Jong and Tom Butynski. Also see Figures 1 and 2.

interpretation concerning the degree of individual variation is due to the examination of a small number of specimens and of a mix of adult and immature specimens.

Intra-subspecific variation in the pelage of *C. m. manyaraensis* is much less than is present in other currently recognized subspecies of *C. mitis* in Kenya and Tanzania, such as *stuhmanni*, *albobularis*, *kolbi*, and *albotorquatus*. Photographs demonstrating this variation can be accessed on the “*Cercopithecus mitis* Photographic Map” at: <www.wildsolutions.nl/photomaps/mitis/>. The considerable variation of the pelage in each of these four subspecies is probably reflected, at least somewhat, by the degree of taxonomic confusion surrounding them, as indicated by the number of species/subspecies synonyms; eight, three, two, and two, respectively. Much of the variation present in the subspecies of *C. mitis* in East Africa and Central Africa (with the exception of *manyaraensis*) can be attributed to the fact that they occur in long phenotypic clines (see below).

Cercopithecus mitis manyaraensis does not occur in a hybrid zone nor does it represent a hybrid swarm

Several authors, including Booth (1968) and Kingdon (1971), indicate that the Manyara Population lies within a *C. mitis* hybrid zone maintained by the secondary contact of *C. mitis* (*stuhmanni* or *doggetti*) from the west side of the ERV with *C. mitis* (*albobularis* or *kolbi*) from the east side of the ERV. Napier (1981, p.97) states, “It appears that members of the *mitis* subspecies group from west of the Rift Valley interbreed with members of the *albobularis* group from the east at the northern end of Lake Manyara...”. Booth (1968) interpreted the Manyara Population as not only occurring in a hybrid zone, but also as a hybrid swarm. Given the state of knowledge concerning the geographic distribution of *C. mitis* in East Africa as of the late 1960s, it seems that Booth (1968), Kingdon (1971), Napier (1981), and others, were unaware of the considerable isolation of the Manyara Population from other subspecies of *C. mitis*.

Hybrid zones are areas of contact between two genetically (and, typically, phenotypically) distinct populations where hybridization occurs (Harrison 1993; Allendorf *et al.* 2001). In certain cases, a hybrid swarm may develop within a hybrid zone, comprised predominantly of hybrids arising from backcrossing with parental types and interbreeding among hybrids. This admixture in the hybrid swarm yields individuals that are highly variable, with genetic and phenotypic characteristics ranging between the two parental types, thereby blurring the boundary between the two parental types (Cockayne and Allan 1926; Allendorf *et al.* 2001; Seehausen 2006; Latch *et al.* 2011). There are at least three observable criteria that can be applied in the field for assessing whether a population is a hybrid swarm. A hybrid swarm can be claimed for a population only if all

three of the following criteria are met: (1) there is a high-level of individual phenotypic variation; (2) both parental types are present; and (3) the population lies in a hybrid zone.

As indicated above, individual variation in the color and pattern of the pelage of *C. m. manyaraensis* is relatively low, being less than is present within other currently recognized subspecies of *C. mitis* in Kenya and Tanzania, and far less than expected of a hybrid swarm.

No one claims to have observed the presence of either of the two parental populations required for maintenance of the putative Manyara Population hybrid zone or hybrid swarm. This study did not find other populations of *C. mitis* within the geographic distribution of the Manyara Population. As such, there are no non-*manyaraensis* pure parental pelage phenotypes in the Manyara Population (i.e., *doggetti*, *stuhmanni*, *albobularis*, *kolbi* pelage phenotypes) that might produce F1 hybrids, and there is no evidence of phenotypic admixture in this population. If this population is the result of secondary contact between *stuhmanni* (or *doggetti*) and *albobularis* (or *kolbi*), that contact is ancient. At present, neither *stuhmanni* nor *albobularis* occurs within 90 km of the Manyara Population. The shortest distance in the region between *stuhmanni* and *albobularis* is *c.* 235 km, roughly 200 km of which is unsuitable habitat composed of semi-arid grasslands and bushlands (Figs. 3 and 4). Based on these findings, it can be concluded that the Manyara Population neither occupies a hybrid zone nor represents a hybrid swarm. *Cercopithecus m. manyaraensis* represents a distinct lineage, but whether this is a taxon of hybrid origin remains an open question.

Booth's hybrids

As mentioned above, Booth (1968) considered *C. m. kolbi* a synonym of *C. m. albobularis*, the subspecies geographically closest to L. Manyara (*c.* 90 km). Phenotypically, *kolbi* is the most distinct of all the *C. mitis* subspecies (Turner *et al.* 1988) and readily distinguished from *C. m. albobularis*. *Cercopithecus m. kolbi* and *albobularis* are geographically isolated from one another by >150 km (Figs. 3 and 4). As such, *kolbi* is considered to be a valid subspecies of *C. mitis* by Groves (2001), Grubb (2001), Grubb *et al.* (2003), Kingdon (2013), Lawes *et al.* (2013), Butynski and De Jong (2017), and De Jong and Butynski (2012, 2018). The population of *C. m. kolbi* closest to L. Manyara is >225 km to the northeast in the Ngong Hills (Figs. 3 and 4). Knowing the provenance of the wild-caught parents and applying current taxonomy, Booth's captive-bred hybrids are the product of *C. m. kolbi* × *C. m. stuhmanni* parents, not *C. m. albobularis* × *C. m. stuhmanni* parents.

Booth (1968) bred and raised eight *C. m. kolbi* × *C. m. stuhmanni* hybrids in captivity at Tigoni Primate Research Centre, Limuru, Kenya (now the Institute of Primate Research, Karen, Nairobi). According to her (p.50), “...all the cage-bred hybrids agree with the specimens from Mto

wa Mbu in being intermediate between *stuhmanni* and *albogularis* [*kolbi*], and it is felt that they strongly support the interpretation of the Ngorongoro and Lake Manyara population as a hybrid swarm.”

Female *C. m. stuhmanni* reach sexual maturity at 5–7 years of age, and males not before seven years of age (Cords and Chowdhury 2010). Booth (1968) described and applied the phenotype of the eight, cage bred, F1 hybrids before any of them reached sexual maturity (the oldest being no more than five years of age). The pelage of immature *C. mitis* changes as adulthood approaches and, therefore, immature individuals are not particularly suitable for phenotypic comparisons against adult individuals. In any case, we disagree with Booth’s claim that the pelage of her F1 hybrids is similar to that of *C. mitis* at Ngorongoro and L. Manyara (i.e., *C. m. manyaraensis*). As demonstrated in Figures 12 and 13, the hybrids differ considerably from *C. m. manyaraensis*, and from any other taxon in the *Cercopithecus* (*nictitans*) Superspecies. The more obvious differences between the hybrids and *C. m. manyaraensis* are that the hybrids have: (1) pelage that has stronger rufous and olive tones, and is shorter, woollier and curlier; (2) ventrum that is not flecked black and grey; and (3) arms and legs with less extensive and less sharply demarcated black and dark grey.

Booth stated that Manyara *C. mitis* are phenotypically similar to her captive-bred *C. mitis kolbi* × *C. mitis stuhmanni* hybrids and that the Manyara Population represents a hybrid swarm. This was widely accepted as strong evidence that *albogularis* (east of the ERV) and *stuhmanni* (west of the ERV) interbreed in the wild and, therefore, are of the same species (i.e., *C. mitis*; Schwarz 1927, 1928, 1954; Allen 1939; Kuhn 1967; Booth 1968; Rahm 1970; Thornton and Groves 1970; Napier 1981;

Kingdon 1971, 1997; Groves 1993; Grubb 2001; Grubb *et al.* 2003; Lawes *et al.* 2013; De Jong and Butynski 2018), and not of two species (i.e., *C. mitis* and *C. albogularis*; Thomas 1900; Pocock 1907; Elliot 1913; Hill 1966; Napier and Napier 1967; Dandelot 1974; Lernould 1988; Groves 2001, 2005; Moulin *et al.* 2008; Kingdon 2013, 2015; Zinner *et al.* 2013a). That the Manyara *C. mitis* are not hybrids, nor representative of a hybrid swarm, means that Booth’s observation is uninformative—not lending support either to assignment of species rank or subspecies rank to *albogularis*.

Habitat and geographic barriers for Cercopithecus mitis in East Africa

Kenya and Tanzania together hold the highest diversity of *C. mitis* subspecies (and their synonyms) of any region. Within these two countries, this diversity is particularly high in southwest Kenya and contiguous northwest Tanzania. The taxonomy and biogeography of *C. mitis* here is, thus, especially complicated. The current distribution of *C. mitis* (Fig. 3) is the outcome of many factors, particularly past geologic and climatic change and the impacts of these changes on the distribution of forest. Two barriers to the movement of *C. mitis* in East Africa appear to be particularly important; one is the ERV (map p.56 in Kingdon [1971]) and the other is unsuitable semi-arid habitat. The areas of semi-arid habitat (i.e., savanna, bushland, open woodland) are not only extensive, they often lack perennial rivers and lakes along which forest might allow dispersal (maps pp.24 and 30 in Kingdon [1971]; maps p.5 in Colyn [1991]; maps pp.47 and 55 in Morley and Kingdon [2013]). As already noted, *C. m. manyaraensis* is encircled and isolated by a vast semi-arid area (Fig. 4).



Figure 12. Comparison of pelage coloration and pattern of an adult female Manyara monkey *Cercopithecus mitis manyaraensis* (center: holotype; ZD.1937.11.8.1) with two captive-bred subadult male *C. m. kolbi* × *C. m. stuhmanni* hybrids (left: ZD.1972.92; right: ZD.1972.94). Courtesy of the Trustees of the Natural History Museum, London. Photographs by Yvonne de Jong and Tom Butynski.



Figure 13. Comparison of pelage coloration and pattern of a captive-bred subadult male *C. m. kolbi* x *C. m. stuhlmanni* hybrid (left: (ZD.1972.92) and an adult male Manyara monkey *Cercopithecus mitis manyaraensis* (paratopotype 1; ZD.1972.90). Courtesy of the Trustees of the Natural History Museum, London. Photographs by Yvonne de Jong and Tom Butynski.

The ERV has long served as a geological barrier to the distribution of forest-dependent primates (Hull 1979; Butynski and De Jong 2007, 2018; Pozzi 2016) and other forest-dependent taxa (Burgess *et al.* 2007; Livingstone and Kingdon 2013) in East Africa due to its considerable depth (1,500 m high escarpment wall in the Kerio Valley), great width (17–35 km across the graben floor and 60–70 km between escarpments), length (*c.* 1,100 km from the north end of L. Turkana to just south of L. Manyara in the vicinity of Mt. Hanang and L. Balangida), high aridity (mean annual rainfall *c.* 400 mm), high temperature (mean maximum temperature *c.* 35°C), and scarcity of forest (Booth 1968; Nyamweru 1996; Bennun and Njoroge 1999; Butynski and De Jong 2007, 2018; Aghová *et al.* 2017). The ERV half-graben terminates near L. Balangida, but major fault lines continue southwards to the Southern Highlands and to the south end of L. Tanganyika (map p.57 in Kingdon [1971]).

The graben floor in East Africa varies from 580 m asl at L. Magadi to 1,890 m asl near L. Naivasha. *Cercopithecus m. manyaraensis* and *C. m. kolbi* are the only two subspecies of *C. mitis* in East Africa found on the floor of the ERV. The only *kolbi* known to occur on the floor of the ERV are in riparian forest at L. Elmenteita (= Elementaita; 1,670 m asl), southwest Kenya (Fig. 4). This population of <100 individuals (K. Combes and P. Mwangi pers. comm.) may still have a tenuous connection with the large population on the Aberdare Range and Mt. Kenya to the east, but remains *c.* 65 km from the nearest known group of *stuhlmanni* in the Mau Forest to the west. Note, however, that an apparently dispersing, solitary, adult male *stuhlmanni* was camera-trapped on 12 September 2018 (C. Wilkinson pers. comm.) in open habitat *c.* 14 km from the nearest group of *kolbi*. What was probably the same solitary male was camera-trapped nearly 6 months later (7 March 2019; C. Wilkinson pers. comm.) in forest along the Nderit R., *c.* 15 km from the nearest group of *kolbi*. The two camera traps were located 4.75 km apart in extreme south Lake Nakuru NP.

Lake Naivasha, 30 km to the southeast of L. Elmenteita, experienced a long episode of climatic stability and relatively high rainfall 155–106 ka (thousand years ago; late Pleistocene), achieving a depth of *c.* 150 m and size of *c.* 520 km². The current lake is 9 m deep and 180 km² (Trauth *et al.* 2001, 2015; Bergner *et al.* 2003). This is coincident with the Eemian Interglacial of 145–120 ka, a time when conditions were wetter, and forest probably extended across tropical Africa from the Atlantic Ocean to the Indian Ocean (Cowling *et al.* 2007). It seems likely that there was a long period of forest connectivity across this part of the ERV centered on 125 ka, perhaps establishing/re-establishing gene flow for *C. mitis*. The climate and forest at L. Naivasha, 300 km north of

L. Manyara, might serve as a proxy to the climate and extent of forest in the Lake Manyara-Ngorongoro Region 155–106 ka. This is perhaps the last time forest connected Mt. Meru and Mt. Kilimanjaro through L. Manyara to the Mau Forest.

While it might be assumed that a member of the Stuhlmanni Section crossed the ERV at least once and that this event eventually gave rise to the Albogularis Section, there is no direct evidence for this. It may be that *C. mitis* reached the east side of the ERV via a distant northern route or (more likely) a southern route, not by crossing the ERV in southwest Kenya. If so, it may be that the members of the Stuhlmanni Section and the Albogularis Section in southwest Kenya are more different than generally supposed. If this is the case, it may be that, if and when they meet at this time, they do not interbreed or, if they do interbreed, this is a rare event and genetic swamping occurs (Kingdon 1971).

Altitudinal limits for *Cercopithecus mitis* in East Africa

As mentioned above, the confirmed altitudinal range of *C. m. manyaraensis* is 960–2,550 m asl, while the probable upper altitudinal limit is around 3,260 m asl. Of the 10 *C. mitis* subspecies known for East Africa, eight occur above 2,550 m asl, while only *stuhlmanni* and golden monkey *C. m. kandti* Matschie, 1906 are confirmed to occur above 3,260 m asl (Table 7). If 3,260 m asl is taken as the upper limit for *manyaraensis*, the altitudinal gradient for this subspecies is 2,300 m. Only *albogularis* and *monoides* have altitudinal gradients >2,300 m. Overall, the altitudinal range for *C. mitis* is 0–3,800 m, which is far greater than for any other forest-dependent cercopithecine (Butynski *et al.* 2013; Morley and

Table 7. Confirmed altitudinal range and gradient for each of the 10 subspecies of *Cercopithecus mitis* known to occur in East Africa (De Jong and Butynski 2018).

Subspecies	Altitudinal range (m asl)	Altitudinal gradient (m)
<i>C. m. kandti</i>	2,100–3,550	1,450
<i>C. m. doggetti</i>	770–2,700	1,930
<i>C. m. stuhlmanni</i>	1,600–3,800	2,200
<i>C. m. manyaraensis</i>	960–2,550 (probably 960–3,260)	1,590 (probably 2,300)
<i>C. m. kolbi</i>	1,000–2,900	1,900
<i>C. m. albotorquatus</i>	0–300	300
<i>C. m. albogularis</i>	0–3,000	3,000
<i>C. m. monoides</i>	0–2,590	2,590
<i>C. m. moloneyi</i>	500–2,600	2,100
<i>C. m. opisthostictus</i>	800–1,800	1,000

Kingdon 2013). This unusual level of adaptability to altitude, and the related great climatic and habitat differences, would have allowed this species to survive many of the more extreme climatic and forest distribution changes of the Pleistocene (see below).

Climate and vegetation in East Africa during the Pliocene and Pleistocene

The climate of tropical Africa from 8–3 Ma (million years ago; late Miocene–mid-Pliocene) was considerably wetter and warmer than today and, as a result, forests were extensive. Subsequently, the period from the mid-Pliocene up to the present has been one of relative climatic extremes and rapid fluctuations, with those after 2.3 Ma (late Pliocene) related to glacials-interglacials. Van Donk (1976) and Hamilton (1988) estimated that there have been 20–21 glacials or near-glacials over the past 2.3 million years (Pleistocene). The last eight glacial-interglacial cycles averaged 100 ka (Maslin and Christensen 2007). The forests of the mid-Pliocene were greatly reduced and fragmented during arid periods that peaked at 3.2, 3.0, 2.8, 1.7, and 1.0 Ma. In between these arid periods were moist periods, particularly from 2.7–2.5 Ma and 1.9–1.7 Ma, when forests expanded and reconnected (deMenocal 1995; Maley 1996; Morley 2000, 2004; Trauth *et al.* 2005; Anhuf *et al.* 2006; Morley and Kingdon 2013). There were particularly prolonged and intense glacial-interglacial cycles of 41–100 ka during 1.0–0.7 Ma (mid-Pleistocene; Maslin and Christensen 2007; Schwartz *et al.* 2012).

Much more recently, in East Africa, there were several “megadroughts” from 115–90 ka (late Pleistocene; Cohen *et al.* 2007; Scholz *et al.* 2007), as well as during the Last Glacial Maximum (24–12 ka); each was accompanied by a reduction of forest. Extremely moist periods, during which forests expanded and reconnected, occurred 145–120, 110–95, 80–65, 55–50, and 35–30 ka (Blome *et al.* 2012). During the Last Glacial Maximum, only islands of forest remained in a landscape composed largely of savanna, bushland, and open woodland. For example, in southwest Kenya, Mt. Elgon had little forest for *c.* 9,000 years (23–14 ka), the Cherangani Hills had no forest for about 15,000 years (28–12 ka), L. Naivasha was almost dry, and L. Victoria was dry. At this time, in East Africa, temperatures dropped 4–8°C, rainfall declined about 30%, and vegetation belts moved downslope 700–1,500 m in altitude (Hamilton 1988; Bonnefille *et al.*, 1990; Hamilton and Taylor 1991; Maitima 1991; Maley 1996; Anhuf 2000; Anhuf *et al.* 2006; Umer *et al.* 2007; Mark and Osmaston 2008; Livingston and Kingdon 2013; Chala *et al.* 2017; Pineiro *et al.* 2017).

The influences of climatic cycles and climatic variability on forest were particularly amplified in East Africa with its steep rainfall and altitudinal gradients,

proximity to the constantly warm Indian Ocean, and an extremely complex topography comprising several large (often deep) lakes (eight of Africa’s nine largest), many mountains (six of Africa’s eight highest), and two great rift valleys. Numerous major tectonic events (i.e., volcanism, up-lifting, rifting) greatly impacted the distribution of forest both directly and indirectly through influences on climate, particularly rainfall (Kingdon 1990; Sepulchre *et al.* 2006; Gani *et al.* 2007; Maslin and Christensen 2007; Spiegel *et al.* 2007; Roberts *et al.* 2012; Schwartz *et al.* 2012; Morley and Kingdon 2013; Ring 2014; Pozzi 2016). Together, these factors would have combined to make the mid-Pliocene–Pleistocene environment of East Africa relatively variable, unstable, and extreme, both temporally and spatially. These are the circumstances under which the *Cercopithecus (nictitans)* Superspecies evolved in East Africa (see below).

Evolutionary history of the Cercopithecus (nictitans) Superspecies

The evolutionary radiation of the Cercopithecini commenced with divergence from the Cercopithecini-Papioni common ancestor *c.* 14–9 Ma (mid-Miocene; Szalay and Delson 1979; Kingdon 1997; Disotell and Raaum 2002; Raaum *et al.* 2005; Tosi *et al.* 2005; Steiper and Young 2006; Perelman *et al.* 2011; Springer *et al.* 2012; Guschanski *et al.* 2013; Zinner *et al.* 2013b). The genus *Cercopithecus* began to rapidly diversify 8.6–7.3 Ma (late Miocene; Disotell and Raaum 2002; Perelman *et al.* 2011; Springer *et al.* 2012; Guschanski *et al.* 2013). Studies of mitochondrial DNA by Guschanski *et al.* (2013) suggest that the ancestor of the *Cercopithecus (nictitans)* Superspecies evolved in Central Africa, splitting from the *Cercopithecus (cephus)* Superspecies *c.* 5.7 Ma (very late Miocene). Rapid species-level diversification within *C. (nictitans)* occurred in Central Africa about 2.4–2.1 Ma (late Pliocene). Several other *Cercopithecus* superspecies also rapidly diversified during the late Miocene–Pliocene (Tosi *et al.* 2005; Springer *et al.* 2012; Guschanski *et al.* 2013; Kingdon and Groves 2013). Subspecies-level diversification within the Stuhlmanni Section of the *Cercopithecus (mitis/albogularis)* Subgroup occurred in Central Africa, west of the Western (Albertine) Rift Valley, *c.* 1.7–0.7 Ma (early to mid-Pleistocene). Subspecies-level diversification with the Albogularis Section occurred in eastern Africa, east of the Western Rift Valley, and in southern Africa, *c.* 0.8–0.3 Ma (mid- to late-Pleistocene; Guschanski *et al.* 2013).

The Pliocene–Pleistocene was also a time of considerable species-level divergence for the majority of other extant genera of African primates, including *Galago*, *Paragalago*, *Otolemur*, *Sciurocheirus*, *Colobus*, *Ptilocolobus*, *Macaca*, *Cercocebus*, *Mandrillus*, *Papio*,

Chlorocebus, and *Homo* (Bobe and Behrensmeyer 2004; deMenocal 2004; Maslin and Christensen 2007; Ting 2008; Perelman *et al.* 2011; Zinner *et al.* 2013b; Pozzi 2016; Rogers *et al.* 2019), many taxa of which are today at least marginally sympatric with members of the *C. (nictitans)* Superspecies (Butynski *et al.* 2013). It seems no coincidence that the relatively rapid evolutionary radiation of the galagids, colobines, cercopithecins, papionins, and hominins of the past 3 million years occurred during a time of relatively large, frequent, variable, and sometimes extreme, climatic fluctuations and tectonic activity during which forests expanded and contracted, sometimes over vast areas (Van Donk 1976; Hamilton 1988; Kingdon 1990; Hamilton and Taylor 1991; deMenocal 1995; Maley 1996; Bobe *et al.* 2002; Bobe and Behrensmeyer 2004; Maslin and Christensen 2007; Bonnefille 2010; Trauth *et al.* 2010; Zinner *et al.* 2011; Kingdon and Groves 2013; Pozzi 2016; Chala *et al.* 2019; Fischer *et al.* 2019; Rogers *et al.* 2019).

There is good evidence that cercopithecins mainly speciated/subspeciated in allopatry (Chapman 1983; Hamilton 1988; Kingdon 1990; Tosi 2008; Kamilar *et al.* 2009; Zinner *et al.* 2011, 2015; Guschanski *et al.* 2013; Chala *et al.* 2019). Climate change and variability during the Pliocene–Pleistocene is widely believed to have been a major driver during the evolutionary history of many African primate taxa through its impacts on the distribution and extent of forest, repeatedly fragmenting, isolating, and reconnecting populations and, thereby, affecting genetic exchange and promoting speciation/subspeciation (Rahm 1970; Kingdon 1971, 1990; Grubb 1978, 1982; Hull 1979; Hamilton 1982, 1988; Colyn 1991; Coe and Skinner 1993; Maley 1996; Morley 2000; Maslin and Christensen 2007; Kamilar *et al.* 2009; Zinner *et al.* 2011, 2015; Blome *et al.* 2012; Guschanski *et al.* 2013; Morley and Kingdon 2013; Pozzi 2016; Chala *et al.* 2019). During periods of isolation, these allopatric populations continued to adapt to ever-changing local conditions, including changes in topography, climate, availability of resources, competition, predators, and pathogens.

Based on the above information, over the past 3 million years, *C. (nictitans)* would have been subjected to numerous forest expansion and retraction events, some of them extreme. After about 0.8 Ma, *C. mitis* probably occurred over almost all of East Africa during the more prolonged interglacials when forest was extensive but restricted to small forest refugia during the more prolonged glacials. More recently, *C. mitis* likely had its greatest geographic distribution in East Africa during the extensive 145–120 ka interglacial and was most restricted during the megadroughts of 115–90 ka and during the Last Glacial Maximum of 24–12 ka.

A second major driver during the evolution of *C. mitis* is probably introgressive hybridization, which appears to be both widespread and frequent in this species. Genetic introgression is not only likely of long standing (Lo Bianco *et al.* 2017), it is on-going; over the past 50 years, field workers have observed *C. mitis* hybrids involving subspecies (Rahm 1970; Kingdon 1971; Colyn 1988, 1991; Twinomugisha *et al.* 2003; T. Butynski and Y. de Jong pers. obs.), species (Dutrillaux *et al.* 1988; Struhsaker *et al.* 1988; Detwiler 2002; Detwiler *et al.* 2005), and genera (De Jong and Butynski 2010c). Episodes of introgressive hybridization, together with repeated fragmentation, isolation, and reconnection of populations, would have promoted the relatively rapid evolution of *C. mitis* and influenced the biogeography of this species.

A further consideration as concerns the evolution and biogeography of *C. mitis* is that, once across the ERV (apparently sometime around 0.8 Ma), this species likely entered a less diverse primate community. This would have “released” *C. mitis* from competition with red-tailed monkey *Cercopithecus ascanius* (Audebert, 1799), L’Hoest’s monkey *Allochrocebus lhoesti* (Sclater, 1899), and grey-cheeked mangabey *Lophocebus albigena* (Gray, 1850), three forest-dependent frugivores for which there are no records east of the ERV (Kingdon 1971; Butynski and De Jong 2007; Butynski *et al.* 2013; De Jong and Butynski 2018). The one forest-dependent monkey that was probably present on the east side of the ERV at the time *C. mitis* crossed, De Brazza’s monkey *Cercopithecus neglectus* Schlegel, 1876, appears to have since been out-competed by *C. mitis* and is now relegated to but one site, the Mathews Range. The Mathews Range is one of the few forested sites east of the ERV where *C. mitis* is absent (De Jong and Butynski 2010). Once across the ERV, new niches, perhaps some of them unoccupied, would have been available to further drive the rapid evolution of *C. mitis*, giving rise to the Albogularis Section and its current complex taxonomy and biogeography.

Geologic history of the Lake Manyara-Ngorongoro Region

The Lake Manyara-Ngorongoro Region lies on the Mbulu Plateau. This plateau is part of a major crystalline basement complex of Precambrian gneiss, some of which is today exposed at the south end of the lake. This region has been geologically active since the late Mesozoic/early Tertiary (65 Ma). Faulting and the associated volcanic activity that began in the mid-Oligocene (30 Ma) gave rise to the ERV in south Kenya and north Tanzania in the mid-Miocene (15–8 Ma), creating the west escarpment and highlands, as well as the c. 100 km-long half-graben “Manyara Basin/Depression” (which now includes both L.

Manyara and L. Burunge). Most of the volcanic cones and craters observed today over the north part of the Mbulu Plateau (e.g., Ngorongoro Crater, Empakaai Crater) were formed during the Pliocene and early Pleistocene (4.9–1.5 Ma), at the same time as Mt. Kilimanjaro, Mt. Meru, Mt. Rungwe, Mt. Kenya, and the Virungas (Bagdasaryan *et al.* 1973; Rodgers *et al.* 1982; Loth and Prins 1986; Ryner *et al.* 2006; Livingstone and Kingdon 2013; Ring 2014). Lake Manyara was established *c.* 1.7–1.0 Ma. At least once in its history, L. Manyara was much deeper (>130 m), covered *c.* 880 km² (four-fold its present size and perhaps connected to L. Natron and L. Magadi to the north), and its east shore was *c.* 40 km farther east than today. The area around L. Manyara has been semi-arid with savanna, woodland, and bushland habitats for at least the past 1.7 Ma (Ring *et al.* 2005; Schwartz *et al.* 2012).

Was the Lake Manyara-Ngorongoro Region a Pleistocene refuge?

The dynamics of the massive loss of forest during the arid and cool glacials, and the emergence of vast arid and semi-arid habitat barriers, likely means that populations within *C. (nictitans)* experienced repeated isolation in forest refugia, and repeated reconnection as forests expanded during the wetter and warmer interglacials. These forest refugia were probably founded on the higher ground favored by prevailing winds bearing moisture westwards from the biggest and deepest inland bodies of water (e.g., L. Kivu, L. Tanganyika, L. Malawi), and on the lower ground bordering the Indian Ocean and the Atlantic Ocean. The most widely recognized, largest, and important Pleistocene refugia in eastern Africa include the highlands along the Western Rift Valley (e.g., Itombwe Massif, Nyungwe Forest, Bwindi Impenetrable Forest, Rwenzori Mts.), the Eastern Arc Mts. (e.g., Taita Hills, East Usambara Mts., Uluguru Mts., Udzungwa Mts., Southern Highlands), and the coastal forests (e.g., Lower Tana R., Arabuko-Sokoke Forest, Shimba Hills, Lindi Coastal Forests).

There appears to be no mention in the literature of the Lake Manyara-Ngorongoro Region serving as a refuge for forest-dependent species at any time during the past 5 million years. This is surprising given the size, altitude, and location of this region. Although L. Manyara NP and Ngorongoro CA are two of the three most visited protected areas in Tanzania, generating considerable foreign exchange and national recognition through tourism (Mwalyosi 1991), the biodiversity they harbour is not well known. This is especially the case for the Ngorongoro CA. Similarly, there is little information on the history of climate change or forest change for the Lake Manyara-Ngorongoro Region. The one study found (Ryner *et al.* 2006) indicates that, based on the pollen record, Empakaai

Crater (3,260 m asl) supported montane forest 14.5–10.1 ka. Presence of forest at the end of the Last Glacial Maximum suggests that montane forest persisted here throughout the arid and cool period of 70–12 ka, and probably throughout the Pleistocene. Drawing heavily from information presented in Hamilton (1982, 1988), Hamilton and Taylor (1991), Blome *et al.* (2012), and Schwartz *et al.* (2020), we postulate the following for the Lake Manyara-Ngorongoro Region for the Pliocene-Pleistocene, and what this might mean for *C. m. manyaraensis*:

Only 400 km from the Indian Ocean and the first area of abruptly rising high ground west of the coastal plain, the extensive Mbulu Plateau (including the Ngorongoro Highlands, the third highest region in Tanzania) received significantly more rainfall, cloud cover, and mist (driven westwards by the Southeast Monsoon coming off the Indian Ocean) than its surroundings. At times, this would have been supplemented by winds transporting moisture off L. Manyara, which was sometimes big at *c.* 880 km². During the most arid and coolest periods, biotic zones shifted downwards about 1,000 m in altitude, putting montane forest on the lower east and south slopes, probably at 1,000–2,300 m asl. That is, montane forest reached the base of the escarpment west of L. Manyara. During the wetter, warmer periods, woodlands and montane forest covered almost all of the east and south slopes from 960–3,260 m asl (similar to the present coverage).

Lake Manyara was dry during the most arid and coolest periods of the past 1.7 million years, but some ground water forest and riparian forest remained as montane forest supported by the large catchment area (7,700 km² today; AWF 2003). It is likely that ground water forest and riparian forest occurred and persisted at the base of the escarpment long before L. Manyara developed. Thus, relative to much of East Africa, there may have been considerable climatic, and therefore environmental, stability and complexity in this area that favoured retention of the most primitive of the *C. mitis* subspecies in East Africa.

The persistence of forest in the Lake Manyara-Ngorongoro Region through the Pleistocene, together with long periods of isolation, would have influenced the evolutionary history of the many forest-dependent species that colonized this region, including *C. m. manyaraensis*.

Based on mitochondrial DNA research (Guschanski *et al.* 2013), *C. mitis* did not reach the ERV before 800 ka (that research did not, however, include *C. m. manyaraensis* samples). As indicated above, there have been several glacial cycles within the past 800 ka and, within the past 145 ka, several megadroughts and extremely wet periods. The most likely forest refugia for *C. mitis* in the region include Mt. Kilimanjaro, Mt. Meru, coastal forests (*C. m. albogularis*) and the Lake Manyara-Ngorongoro Region (*manyaraensis*), with the Lake Manyara-Ngorongoro Region being the most isolated.

Origin and phylogenetic affinities of Cercopithecus mitis manyaraensis

Against the above background, we put forth two hypotheses for the origin of *C. m. manyaraensis* in the Lake Manyara-Ngorongoro Region.

Hypothesis I: *Cercopithecus mitis manyaraensis* represents a now isolated section of a phenotypic cline across the Eastern Rift Valley. Coloration and pattern of the pelage of *C. mitis* varies clinally over vast areas of East Africa and Central Africa. Two major phenotypic clines occur over this region (Figs. 1–3; Table 1). On the east side of the ERV there is a phenotypic cline in the Albogularis Section that extends from the Ngong Hills of central south Kenya north through the Aberdare Range and Mt. Kenya (*kolbi*), then east and south along the Tana R. (*albotorquatus*), then down the coastal plain of south Kenya and northeast Tanzania (*albogularis*), then west along the Rufiji R. to the escarpment of the Udzungwa Mts. (*monoides*), then southwest through the Udzungwa Mts. to the Southern Highlands of southwest Tanzania, then south through the highlands of north Malawi and northeast Zambia (*moloneyi*), then west into southwest DRC and north Zambia (*opisthostictus*). There are no fewer than six currently recognized subspecies (none of them particularly isolated) along this phenotypic cline. In addition, there appears to be a, now much fragmented, phenotypic cline from the Aberdare Range and Mt. Kenya (*kolbi*) south through Machakos then southeast around the Taru Desert via Kibwezi, Chyulu Hills, Mzima Springs, and Tsavo R. (and then perhaps via Magoine R., and/or Ngara Len R.) in central south Kenya to Mt. Meru and Mt. Kilimanjaro in northeast Tanzania and Taita Hills in southeast Kenya (*albogularis*) (B. Finch pers. comm.; S. Marisia pers. comm.; S. Thomsett pers. comm.).

On the west side of the ERV, and then along the Western Rift Valley, there is an even more complex phenotypic cline in the Stuhlmanni Section that extends from north DRC and southwest Uganda (*stuhlmanni* and *doggetti*), south through Rwanda and Burundi (*doggetti* and *kandti*) into southwest DRC and north Zambia

(*opisthostictus*). There are no fewer than four currently recognized subspecies (none of them particularly isolated) along this phenotypic cline.

The primary barrier that separates the Albogularis Section Cline from the Stuhlmanni Section Cline through southwest Kenya and northwest Tanzania is the arid/semi-arid floor of the ERV (the south end of which is in the vicinity of L. Balangida; Ring *et al.* 2005; Schwartz *et al.* 2012). Elsewhere, vast regions of unsuitable arid habitat separate these two clines until the south end of L. Tanganyika is reached. There these two phenotypic clines (apparently) converge, with *moloneyi* meeting *opisthostictus*. Geotagged photographs of *C. mitis* along these clines in East Africa can be accessed on the “*Cercopithecus mitis* Photographic Map” at: <www.wildsolutions.nl/photomaps/mitis/>.

Even today, after considerable anthropogenic degradation, destruction, and fragmentation of forest across East Africa, the major Albogularis Section Cline and the Stuhlmanni Section Cline remain continuous, or nearly so. Along these two clines there are, however, human-created forest fragments (some of them big) in which *C. mitis* occurs, probably in genetic isolation. It is likely that both of these clines were broadly continuous <150 years ago. It appears that the only subspecies of *C. mitis* in East Africa that is currently not part of either cline is *manyaraensis*.

Over much of the length (*c.* 1,600 km²) of the ERV through Kenya and north Tanzania, the subspecies in the Albogularis Section and the subspecies in the Stuhlmanni Section do not come close to meeting across the semi-arid floor of the ERV. The only subspecies of *C. mitis* on the floor of the ERV in Kenya and Tanzania between the north end of L. Turkana in southwest Ethiopia (where *boutourlinii* is isolated) and L. Manyara are *kolbi* and *manyaraensis*. Although neither subspecies occurs completely across the ERV at this time, their presence on the floor of the ERV may be an indication of where subspecies in the Albogularis Section and subspecies in the Stuhlmanni Section last had connectivity across the ERV (if they ever had connectivity).

Based on pelage alone, phenotypically intermediate *manyaraensis* cannot be allocated to either the Stuhlmanni Section or the Albogularis Section, but can be envisioned as perhaps once serving as part of a cline across the ERV between *stuhlmanni* (or another subspecies) in the west and *albogularis* (or another subspecies) in the east. This would have been during one or more of East Africa’s wettest periods when a forest corridor across the ERV likely connected Mt. Meru/Mt. Kilimanjaro to the Mau Escarpment via L. Manyara and the Ngorongoro Highlands. As indicated above, the wettest periods during which massive forest expansion likely occurred were

during the interglacials of 145–120 ka, 110–95 ka, 80–65 ka, 55–50 ka, and 35–30 ka, with forest expansion being particularly extensive during 145–120 ka. It may be that *manyaraensis* represents a now isolated part of this phenotypic cline as a result of the withdrawal and fragmentation of sections of this cline caused by a drier and cooler climate and the emergence of semi-arid vegetation barriers.

Hypothesis II: *Cercopithecus mitis manyaraensis* is a close relative of *C. mitis opisthostictus* and, thereby, is a relic of dispersal from the Congo Basin/Upper Zambezi Basin to the Lake Manyara-Ngorongoro Region. Based on coloration and pattern of the pelage, *C. m. manyaraensis* is the most different of the subspecies of the *C. mitis* known for East Africa. Phenotypically, *manyaraensis* is most similar to *C. m. opisthostictus* (Figs. 1, 2 and 11) of the southeast Congo Basin and Upper Zambezi Basin. *Cercopithecus m. opisthostictus*, a member of the Opisthostictus Section, reaches Tanzania at the southeast corner of L. Tanganyika (*c.* 740 km southwest of L. Manyara; Fig. 3). Based on chromosome number (*nictitans* and *opisthostictus*: $2n = 70$; *mitis*: $2n = 72$ [Dutrillaux *et al.* 1980, 1982, 1988; Sineo 1990; Moulin *et al.* 2008]) and mitochondrial DNA findings (Guschanski *et al.* 2013), *opisthostictus* is basal to *C. (nictitans)*. This, and a divergence time of *c.* 2.4 Ma, suggest that *opisthostictus* deserves species status along with *C. nictitans* and *C. mitis* (Kingdon 2013). If *manyaraensis* derived from *opisthostictus*, its dispersal from the Congo Basin/Upper Zambezi Basin to the Lake Manyara-Ngorongoro Region during the Pleistocene is likely along what is referred to as the “Southern Route” (Kingdon 1971, 1990; Rodgers *et al.* 1982; Tosi 2006)—the route believed to have been used by plants and animals dispersing from the “Southern Congo Basin Refuge” (Kingdon 1980; Hamilton 1988) in southeast DRC eastwards around the south end of L. Tanganyika through Tanzania and north up the coasts of Tanzania, Kenya, and Somalia. Kingdon (1981) considers the Southern Route to be particularly ancient. The Southern Route eastwards through Tanzania seems more likely than the “Northern Route”, as east of the south end of L. Tanganyika there is a long corridor of forested high ground (that includes the sizeable L. Rukwa) to the Southern Highlands, then a large area of high ground over the Southern Highlands and Udzungwas that gives rise to the extensive Ruaha-Rufiji River System, the riparian forests of which might have served as corridors through the vast arid littoral to the coast (map p.9 in Kingdon [1971]). This region from L. Tanganyika to the Indian Ocean would have been forested during the wetter periods of the Pliocene and Pleistocene.

It appears that *C. m. manyaraensis* is a member of the Opisthostictus Section. Kingdon (2013) suggests that

C. m. opisthostictus is the direct descendent of the founding *C. (nictitans)* lineage and that it continues to live in at least part of the region in which the ancestors of this superspecies emerge (i.e., southern Central Refuge of southeast Congo Basin and Upper Zambezi Basin). We suspect that *manyaraensis* represents a relic population, and that its presence in the Lake Manyara-Ngorongoro Region pre-dates the arrival of other *C. mitis* at the ERV about 0.8–0.3 Ma (Guschanski *et al.* 2013). It may even be that *manyaraensis* represents an ancient form from which the subspecies of *C. mitis* east and/or west of the ERV radiated. Molecular studies are required to better understand the evolutionary history of *C. mitis* in East Africa, particularly *manyaraensis*. In this regard, perhaps a first step would be to determine the chromosome number ($2n$) for *C. m. manyaraensis*, and to confirm that the chromosome number for *C. m. opisthostictus* is 70. If $2n = 70$ in both, this would imply a close, basal, relationship, and some distinction from other taxa within *C. (nictitans)* (as far as is known, except for *C. nictitans* and *opisthostictus*, all other taxa within this superspecies are $2n = 72$; Kuhn 1967; Dutrillaux *et al.* 1980, 1982, 1988; Sineo 1990; Moulin *et al.* 2008).

Taxonomic arrangement of Cercopithecus mitis manyaraensis

Reliable information on the taxonomic status of populations is critical to setting priorities for the conservation of species (Mace 2004; Zinner and Roos 2016; Gippoliti *et al.* 2018). A good understanding of the taxonomy and biogeography of *C. mitis* is not only of considerable scientific interest, it is important to the conservation of the high diversity found within this species.

As indicated above, *C. m. manyaraensis* is: (1) geographically isolated from other *C. mitis* (>90 km) by semi-arid vegetation barriers; (2) phenotypically distinct from other subspecies of *C. mitis*; and (3) presents little inter-individual variation. As such, the diagnosable phenotypic characters of *C. m. manyaraensis* appear to be fixed, genetic, and heritable. Therefore, the Manyara monkey should no longer be considered a hybrid, but rather a subspecies of *C. mitis*. In fact, under the “Phylogenetic Species Concept” (Cracraft 1983, 1992; Groves 2001, 2004; Groves and Hapold 2013), the Manyara monkey deserves recognition as a species—*Cercopithecus manyaraensis*. However, given that the taxonomic classification of *C. mitis* is currently contentious and under debate (Kingdon 2013, 2015; Groves 2001, 2005; Grubb 2001; Grubb *et al.* 2003; Lawes *et al.* 2013; Zinner *et al.* 2013a; De Jong and Butynski 2018), and that additional biogeographical research and, particularly, deep molecular research, are required to

further our understanding of the taxonomy of *C. mitis*, species designation may be premature.

Conservation of Cercopithecus mitis manyaraensis

Tanzania is one of the most important countries in Africa for primate conservation (De Jong and Butynski 2012, 2018; Davenport *et al.* 2013; IUCN 2020) given its large number of non-human primates—14 genera, 28 species, and 44 species and subspecies, including *C. m. manyaraensis*. Of these, six monotypic species and seven subspecies are endemic to Tanzania. Eleven species and eight subspecies are classified as threatened on the IUCN Red List (2020); nine “Vulnerable”, eight “Endangered”, and two “Critically Endangered”. Two “Data Deficient” subspecies will probably be assessed as threatened once the required data become available.

Most species of primate in Tanzania are forest-dependent. As such, Tanzania is in danger of losing several primate species and subspecies. Tanzania has the second highest rate of forest loss in sub-Saharan Africa (FAO 2005). During 1990–2010, Tanzania lost 4,034 km² (1.1%) of its forest each year (FAO 2010). Tanzania’s human population growth remains high at 3.0% (PRB 2019). The 2019 population of 58 million people is projected to increase to 90.4 million by mid-2035 and to 129.4 million by 2050 (PRB 2019). Given this trend, and the rapidly growing demand for land and forest products, it is inevitable that Tanzania will continue to lose large areas of forest.

The forests of L. Manyara NP and Ngorongoro CA are vital for the long-term conservation of *C. m. manyaraensis*, but these forests are under threat. The human population in the vicinity of L. Manyara NP increased nearly six-fold in but 21 years, from 6.5 people/km² in 1967 to 37.9 people/km² in 1988. At Mto wa Mbu, the human population increased more than 35-fold in 76 years, from 500 people in 1943 (Mwalyosi 1991) to 17,754 in 2019 (WPR 2019). In the Ngorongoro CA, the human population increased nine-fold in just 46 years (from 8,700 in 1966 to 79,000 in 2012), while the number of livestock in 2012 was 300,000 (IUCN 2014). Whereas there was probably no land under cultivation in the Ngorongoro CA in 1950, 177 km² were under cultivation in 2000, most of which was previously forest (Niboye 2010). People in and around both of these protected areas continue to look towards the forests for wood products and farmland.

Approximately 60% (3,500 km²) of the probable geographic distribution of *C. m. manyaraensis* lies within six protected areas (Ngorongoro CA, L. Manyara NP, Nou CFR, Hassama Hill FR, Ufiome FR, and Burunge Wildlife Management Area [WMA]; Fig. 10). The region’s rapidly growing human population has led to the degradation, loss,

and fragmentation of natural habitats, both outside and within protected areas, for farmland, timber, building poles, fuelwood, charcoal, roads, dams, mining, exotic tree plantations, human settlements, and grass and browse for domestic livestock. In addition, there is an increase in poaching of animals, fire, disease transmission, and invasion of exotic plants. These activities have cascading effects, damaging the region’s soils, water availability and quality, wildlife migration corridors, biological productivity, and biodiversity (Mwalyosi 1991; AWF 2003; Niboye 2010; IUCN 2014; Kiffner *et al.* 2015, 2017; Debonnet and Nindi 2017). This undermining of ecosystem services has major negative effects on the well-being of people and on their opportunities for sustainable development.

The connectivity among the six protected areas in which *C. m. manyaraensis* is known to occur is threatened (Fig. 10). Most important is the Manyara-Ngorongoro Wildlife Corridor (also known as the “Upper Kitete/Selela Wildlife Corridor”). Once connecting Manyara NP and Ngorongoro CA, this 2-km-wide × 10-km-long corridor has been lost to agriculture, settlements, and other activities (Mwalyosi 1991). Given its location between two large, biologically diverse, and economically important protected areas, the Manyara-Ngorongoro Wildlife Corridor has extremely high conservation value. Some efforts are being made to restore this corridor but this will be challenging as the number of people and livestock in the area continue to increase and land-use intensifies (Debonnet and Nindi 2017). As concerns the conservation of *C. m. manyaraensis*, the priority is the restoration of the Manyara-Ngorongoro Wildlife Corridor and protection of its ground water forest and riparian forest.

When assessed in 2016 for the IUCN Red List of Threatened Species (IUCN 2012), the category of threat for the Manyara monkey, *Cercopithecus mitis*, ssp. nov., was Endangered; B1ab(i,ii,iii). Although *C. m. manyaraensis* is locally common, the “Extent of Occurrence” is c. 4,600 km². The “Extent of Occurrence”, “Area of Occupancy”, quality of habitat, and number of mature individuals are all projected to continue to decline (De Jong and Butynski 2020).

Cercopithecus m. manyaraensis is broadly sympatric with four other primates: olive baboon *Papio anubis* (Lesson, 1827); Hilgert’s vervet *Chlorocebus pygerythrus hilgerti* (Neumann, 1902); Uganda lesser galago *Galago senegalensis sotikae* Hollister, 1920; and Pangani small-eared galago *Otolemur garnettii panganiensis* Matschie, 1906 (Appendix V). As such, actions to conserve *C. m. manyaraensis* will also benefit these four species.

Research Priorities

We propose three research priorities for *C. m. manyaraensis*:

1. Several taxonomic questions raised in this paper will not be answered without substantially more genomic information about the *Cercopithecus (nictitans)* Superspecies. Comparative molecular research should be conducted on all recognized taxa within *C. (nictitans)* in order to clarify the taxonomic arrangement and phylogeography of the species and subspecies in this superspecies, as well as assess the level of genetic variation within each taxon. This information will provide guidance for setting research and conservation priorities. Knowledge of the timing of divergence events will yield insights into the environmental history of Africa during the late Pliocene-Pleistocene. Like *Papio*, *C. (nictitans)* diversified rapidly during the Pleistocene, but being a forest-dependent species, it would have been differently affected, both temporally and spatially, by the climate changes of this period. As for *Papio*, hybrid introgression probably played a major role in the evolution of *C. (nictitans)*. With the exception of *Papio*, probably no taxonomic group of African primates has more potential to reveal the dynamics of Pliocene-Pleistocene climates and environments than does *C. (nictitans)*, nor more potential to contribute, as a “model organism,” to the understanding of the role of hybrid introgression in primate evolution, including the evolution of *Homo* (Ackermann *et al.* 2019).

2. Forests in the following areas are priorities for preliminary ground surveys to determine presence/absence of *C. m. manyaraensis*: Salanga FR, Bereku FR, Haraa FR, Makonge Hill, areas to the west and east of the north end of Lake Eyasi, Losiminguri FR, area east of Mto wa Mbu, Kitombeine FR, Gelai FR (Fig. 10). Once presence has been confirmed, all sites with *manyaraensis* should be further surveyed to determine geographic distribution, abundance, and threats (IUCN 2012). This information will improve the baseline for the long-term monitoring of this subspecies and serve the next IUCN Red List category of threat assessment.

3. Forests of the Lake Manyara-Ngorongoro Region need to be accurately mapped to establish a better baseline for the conservation monitoring of *C. m. manyaraensis*, and for identifying gaps in forest corridors that might isolate populations in Ngorongoro CA, L. Manyara NP, Darakuta Ranch, Nou CFR, Hassama Hill FR, Ufiome FR, Burunge WMA, and other sites where this subspecies occurs. Are there forest corridors along the floor of the ERV and/or along the wall of the escarpment? What are the threats to the forest corridors?

Conclusions

The most important conclusions of this study are:

1. Manyara *C. mitis* is geographically isolated from other *C. mitis* by >90 km of semi-arid habitat, is phenotypically distinct from other *C. mitis*, and exhibits little intra-population variation.

2. There is no evidence for clinal phenotypic variation across the geographic distribution of the population of Manyara *C. mitis*.

3. Manyara *C. mitis* is not a hybrid, it does not lie in a hybrid zone, nor does it represent a hybrid swarm.

4. Manyara *C. mitis* is morphologically unique and, therefore, genetically unique. As such, it represents a distinct lineage. Here we name this subspecies the Manyara monkey *Cercopithecus mitis manyaraensis*.

5. *Cercopithecus m. manyaraensis* is endemic to Tanzania. The known geographic distribution is c. 1,480 km². The probable geographic distribution is roughly 5,865 km², including c. 2,055 km² of protected forest. Roughly 60% (3,500 km²) of the probable geographic distribution lies within six protected areas. Within the probable geographic distribution, the altitude ranges from 960 m asl to 3,260 m asl and mean annual rainfall ranges from 500 mm to 1,200 mm.

6. The main threats to *C. m. manyaraensis* are habitat degradation, loss, and fragmentation related to the region’s rapidly increasing human population. The current IUCN Red List of Threatened Species category of threat for *C. m. manyaraensis* is Endangered.

7. Conservation priorities for *C. m. manyaraensis* include the effective management of the six protected areas in which it occurs, and the restoration and protection of the wildlife corridors of the Lake Manyara-Ngorongoro Region.

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Appendix I

Some of the more common tree species in the Lake Manyara Study Area and Loita-Nguruman Study Area. Arranged in alphabetical order by family.

Ngorongoro Conservation Area

(Baker and Baker 2002; Ryner *et al.* 2006; BirdLife 2019b; T. Butynski and Y. de Jong pers. obs.)

Araliaceae

Polyscias fulva (Hiern) Harms

Cupressaceae

Juniperus procera Hochst. ex Endl.

Euphorbiaceae

Croton macrostachyus Hochst. ex Delile

Croton megalocarpus Hutch.

Macaranga kilimandscharica Pax

Loganiaceae

Nuxia congesta R. Br. ex Fresen.

Mimosaceae

Acacia lahai Steud. & Hochst. ex Benth.

Albizia gummifera (J. F. Gmel.) C. A. Sm.

Oleaceae

Olea europaea L.

Pittosporaceae

Pittosporum goetzei Engl.

Podocarpaceae

Podocarpus latifolius (Thunb.) R. Br. ex Mirb

Rhizophoraceae

Cassipourea malosana (Baker) Alston

Rosaceae

Hagenia abyssinica (Bruce) J. F. Gmel.

Rutaceae

Vepris simplicifolia (Engl.) Mziray

Ulmaceae

Celtis africana Burm. f.

Lake Manyara National Park (excluding Marang Forest)

(Greenway and Vesey-Fitzgerald 1969, 1972; Loth and Prins 1986; Loth 1999; T. Butynski and Y. de Jong pers. obs.)

Apocynaceae

Rauvolfia caffra Sond.

Tabernaemontana ventricosa Hochst. ex A. DC.

Balanitaceae

Balanites aegyptiacus (L.) Delile

Bignoniaceae

Kigelia africana (Lam.) Benth.

Bombacaceae

Adansonia digitata L.

Boraginaceae

Cordia africana Lam.

Cordia sinensis Lam.

Burseraceae

Commiphora africana (A. Rich.) Engl.

Commiphora baluensis Engl.

Commiphora longipedicellata Vollesen

Commiphora schimperi (O. Berg) Engl.

Canellaceae

Warburgia ugandensis Sprague

Capparaceae

Maerua triphylla A. Rich.

Combretaceae

Terminalia brownii Fresen.

Combretum molle R. Br. Ex G. Don

Euphorbiaceae

Bridelia micrantha (Hochst.) Baill.

Croton macrostachyus Hochst. ex Delile

Euphorbia candelabrum Trémaux ex Kotschy

Guttiferae

Garcinia livingstonei T. Anderson

Meliaceae

Trichilia emetica Vahl.

Mimosaceae

Acacia albida Delile

Acacia hockii De Wild.

Acacia mellifera (Vahl) Benth.

Acacia sieberiana DC.

Acacia tortilis (Forssk.) Hayne

Acacia xanthophloea Benth.

Moraceae

Antiaris toxicaria (Pers.) Lesch.

Ficus natalensis Hochst.

Ficus sycomorus L.

Ficus wakefieldii Hutch.

Myrtaceae

Syzygium guineense (Willd.) DC.

Palmae

Phoenix reclinata Jacq.

Rubiaceae

Gardenia volkensii K. Schum.

Sterculiaceae

Sterculia africana (Lour.) Fiori

Ulmaceae

Celtis africana Burm. f.

Trema orientalis (L.) Blume

Marang Forest (within Lake Manyara National Park)

(Loth 1999; Baker and Baker 2002; BirdLife 2019a)

Euphorbiaceae

Macaranga kilimandscharica Pax

Meliantaceae

Bersama abyssinica Fresen.

Mimosaceae

Acacia tortilis (Forssk.) Hayne

Albizia gummifera (J. F. Gmel.) C. A. Sm.

Oleaceae

Olea capensis L.

Olea europaea L.

Podocarpaceae

Podocarpus latifolius (Thunb.) R. Br. ex Mirb

Rutaceae

Clausena anisata (Willd.) Hook. f. ex Benth.

Nou Catchment Forest Reserve

(Farm Africa 2019)

Lauraceae

Ocotea usambarensis Engl.

Podocarpaceae

Podocarpus latifolius (Thunb.) R. Br. ex Mirb

Rutaceae

Fagaropsis angolensis (Engl.) Dale

Mount Hanang Nature Forest Reserve

(TFS 2016; T. Butynski and Y. de Jong pers. obs.)

Araliaceae
Cussonia holstii Harms ex Engl.
 Celastraceae
Catha edulis (Vahl) Forssk.
 Cupressaceae
Juniperus procera Hochst. ex Endl.
 Euphorbiaceae
Croton macrostachyus Hochst. ex Delile
Macaranga kilimandscharica Pax
 Loganiaceae
Nuxia congesta R. Br. ex Fresen.
 Meliaceae
Ekebergia capensis Sparrm.
 Mimosaceae
Acacia mearnsii De Wild.
Acacia tortilis (Forssk.) Hayne
Albizia gummifera (J. F. Gmel.) C. A. Sm.
 Moraceae
Ficus sur Forssk.
Ficus thonningii Blume
 Myrtaceae
Eucalyptus spp.
 Rosaceae
Hagenia abyssinica (Bruce) J. F. Gmel.
 Rutaceae
Calodendrum capense Thunb.
Fagaropsis angolensis (Engl.) Dale
 Ulmaceae
Celtis africana Burm. f.

Loita-Nguruman Hills

(Maundu *et al.* 2001; Karanja *et al.* 2002; Butynski and De Jong 2012)

Apocynaceae
Acokanthera schimperi (A. DC.) Schweinf.
 Araliaceae
Cussonia holstii Harms ex Engl.
Cussonia spicata Thunb.
 Bignoniaceae
Kigelia africana (Lam.) Benth.
 Burseraceae
Commiphora spp.
 Canellaceae
Warburgia salutaris (G. Bertol.) Chiov.
 Celastraceae
Maytenus heterophylla (Eckl. & Zeyh.) N. Robson
Mystroxydon aethiopicum (Thunb.) Loes.
 Compositae
Tarchonanthus camphoratus L.

Cupressaceae
Juniperus procera Hochst. ex Endl.
 Ebenaceae
Diospyros abyssinica (Hiern) F. White
 Ericaceae
Agauria salicifolia (Comm. ex Lam.) Hook. F. ex Oliv.
 Euphorbiaceae
Croton macrostachyus Hochst. ex Delile
Euphorbia candelabrum Trémaux ex Kotschy
 Flacourtiaceae
Flacourtia indica (Burm. f.) Merr.
 Loganiaceae
Nuxia congesta R. Br. ex Fresen.
 Meliaceae
Ekebergia capensis Sparrm.
 Melianthaceae
Bersama abyssinica Fresen.
Trichilia sp.
 Mimosaceae
Acacia drepanolobium Harms ex Y. Sjöstedt
Acacia gerrardii Benth.
Acacia hockii De Wild.
Acacia kirkii Oliv.
Acacia nilotica (L.) Willd. ex Delile
Acacia seyal Delile
 Moraceae
Ficus thonningii Blume
 Myrtaceae
Syzygium cordatum Hochst. in C. Krauss
Acacia xanthophloea Benth.
 Ochnaceae
Tarchonanthus camphoratus L.
 Oleaceae
Olea capensis L.
Olea europaea L.
Schrebera alata (Hochst.) Welw.
 Palmae
Phoenix reclinata Jacq.
 Papilionaceae
Erythrina abyssinica Lam. ex DC.
 Podocarpaceae
Podocarpus latifolius (Thunb.) R. Br. ex Mirb
Podocarpus falcatus (Thunb.) R. Br. ex
 Rhizophoraceae
Cassipourea malosana (Baker) Alston
 Rubiaceae
Gardenia volkensii K. Schum.
 Rutaceae
Fagaropsis angolensis (Engl.) Dale
Teclea simplicifolia (Engl.) I. Verd.
Zanthoxylum usambarensis (Engl.) Kokwaro
 Sapindaceae
Pappea capensis Eckl. & Zeyh.

Appendix II

The 88 specimen skins of gentle monkey *Cercopithecus mitis* from East Africa, Zambia, and DRC directly examined by the authors at the Natural History Museum, London (45 specimens), The National Museums of Kenya, Nairobi (22), Royal Museum for Central Africa, Tervuren (15), and American Museum of Natural History, New York (6). These include nine holotypes, two lectotypes, and two paralectotypes. The taxonomy applied here is that of Grubb *et al.* (2003) and Laws *et al.* (2013). The 10 specimens with an asterisk before the accession number are Manyara *C. mitis*. Information presented here provided by specimen tags, collection curators, Napier (1981), Natural History Museum (2014), Trombone (2016), and the authors.

Subspecies	Accession number	Locality	Altitude m (ft)	Age/sex	Date collected	Collector
Natural History Museum, London, UK						
Intermediate between <i>C. m. albogularis</i> and <i>C. m. stuhlmanni</i>	ZD.1937.11.8.1*	North end L. Manyara, central north Tanzania	960 (3,150)	Adult female	1 May 1937	B. Cooper
Intermediate between <i>C. m. albogularis</i> and <i>C. m. stuhlmanni</i>	ZD.1951.371*	Kirurumo R. near Mto wa Mbu, L. Manyara, central north Tanzania	975 (3,200)	Adult female	5 Sep 1948	G. H. Swynnerton
Intermediate between <i>C. m. albogularis</i> and <i>C. m. stuhlmanni</i>	ZD.1972.89*	Mto wa Mbu, L. Manyara, central north Tanzania	975 (3,200)	Subadult female	13 Nov 1963	C. P. Booth (see Booth 1968)
Intermediate between <i>C. m. albogularis</i> and <i>C. m. stuhlmanni</i>	ZD.1972.90*	Mto wa Mbu, L. Manyara, central north Tanzania	975 (3,200)	Adult male	13 Nov 1963	C. P. Booth (see Booth 1968)
<i>C. m. kolbi</i>	ZD.1900.1.3.1 holotype	Kedong Escarpment, central south Kenya	c. 2,200 (7,220)	Adult male	21 Sep 1899	C. S. Betton
<i>C. m. kolbi</i>	ZD.1900.2.1.4 holotype <i>nubilus</i>	Nairobi Forest, central south Kenya	c. 1,700 (5,580)	Adult female	14 Jul 1899	J. Mackinder
<i>C. m. kolbi</i>	ZD.1903.5.25.1 holotype <i>hindei</i>	Tuthu (=Tusu R.), central south Kenya	2,400 (8,000)	Adult male	Dec 1902	S. L. Hinde
<i>C. m. kolbi</i>	ZD.1950.12	Mt. Kenya, central Kenya	1,830 (6,000)	Adult male	28 Nov 1941	C. Schultz
<i>C. m. albotorquatus</i>	ZD.1912.7.10.1	Sankuri R., near Tana R., central east Kenya	240 (787)	Juvenile male	?	G. Blaime
<i>C. m. albotorquatus</i>	ZD.1949.580	Kalifi Forest (=Kilifi), south coast, Kenya	0 (0)	Adult male	13 Apr 1949	Col. Zool. Soc. London
<i>C. m. albotorquatus</i>	ZD.1951.690	Saka, Tana R., central east Kenya	455 (1,500)	Adult male	14 Aug 1951	C. H. Stockley
<i>C. m. albotorquatus</i>	ZD.1951.691	Saka, Tana R., central east Kenya	455 (1,500)	Juvenile male	14 Aug 1951	C. H. Stockley
<i>C. m. albogularis</i>	ZD.1855.12.24.13 holotype	Fixed by Schwarz (1927) as Zanzibar, Indian Ocean, east Tanzania	0-120 (0-390)	Adult male	Pre-1832	W. H. Sykes
<i>C. m. albogularis</i>	ZD.1908.9.26.1	Moshi, Kilimanjaro, northeast Tanzania	700 (2,297)	Adult male	Feb 1902	A. P. Percival
<i>C. m. albogularis</i>	ZD.1917.8.21.3	R. Savo (Tsavo), Mt. Kilimanjaro, southeast Kenya	550 (1,800)	Adult female	2 Aug 1914	H. Praed
<i>C. m. albogularis</i>	ZD.1917.8.21.4	R. Savo (Tsavo), Mt. Kilimanjaro, southeast Kenya	550 (1,800)	Adult female	2 Aug 1914	H. Praed
<i>C. m. albogularis</i>	ZD.1920.6.10.1	Tumbatu Island, Zanzibar, Indian Ocean, east Tanzania	6 (20)	Adult male	8 May 1919	H. H. Swinny
<i>C. m. albogularis</i>	ZD.1935.10.18.4	Usa, Mt. Meru, central north Tanzania	1,300 (4,265)	Adult male	1935	D. Bagster Wilson
<i>C. m. albogularis</i>	ZD.1964.1015	Bweleo, Zanzibar Island, Indian Ocean, east Tanzania	15 (49)	Adult male	6 Aug 1954	W. H. R. Lumsden

<i>C. m. albogularis</i>	ZD.1972.51	3 km north of Chwaka, Zanzibar Island, Indian Ocean, east Tanzania	0 (0)	Juvenile female	3 Dec 1959	C. P. Booth
<i>C. m. albogularis</i>	ZD.1972.52	Diani Beach, extreme southeast Kenya	0 (0)	Adult male	27 Dec 1962	C. P. Booth
<i>C. m. monoides</i>	ZD.1878.12.26.1 lectotype <i>rufilatus</i>	Rufiji R., central coast east Tanzania	0-200 (0-660)	Adult male	Pre-1879	B. Wharton
<i>C. m. monoides</i>	ZD.1878.12.26.2 paralectotype <i>rufilatus</i>	Rufiji R., central coast east Tanzania	0-200 (0-660)	Adult female	Pre-1879	B. Wharton
<i>C. m. monoides</i>	ZD.1922.7.17.1	Morogoro, central east Tanzania	610 (2,000)	Juvenile female	17 Aug 1917	L. D. Swaythling
<i>C. m. monoides</i>	ZD.1933.6.14.1	Mafia Island, Indian Ocean, east Tanzania	15 (50)	Adult male	26 Mar 1933	W. V. Harris
<i>C. m. moloneyi</i>	ZD.1966.21 ?neotype	Near Karonga, northwest shore of L. Nyasa (=L. Malawi), Malawi	c. 480 (1,570)	Adult male	Apr 1892	A. Whyte
<i>C. m. stuhlmanni</i>	ZD.1906.7.1.1 holotype <i>carruthersi</i>	Ruwenzori, east side, southwest Uganda	3,050 (10,000)	Juvenile female	9 Jan 1906	D. Carruthers
<i>C. m. stuhlmanni</i>	ZD.1907.4.6.6 holotype <i>princeps</i>	Mpanga Forest, Fort Portal, southwest Uganda	1,525 (5,000)	Adult male	23 Sep 1906	R. D. Dent
<i>C. m. stuhlmanni</i>	ZD.1972.72	Kakamega, southwest Kenya	1,525 (5,000)	Adult male	8 Sep 1962	A. Rivers-Thomas and C. P. Booth
<i>C. m. stuhlmanni</i>	ZD.1972.76	Marindas Forest, Eastern Mau FR, southwest Kenya	2,740 (9,000)	Adult male	28 Jul 1960	C. P. Booth
<i>C. m. stuhlmanni</i>	ZD.1972.82	Kaptagat, Mt. Elgon, southwest Kenya	2,440 (8,000)	Adult male	?	C. P. Booth
<i>C. m. doggetti</i>	ZD.1904.8.1.1 holotype	Southwest Ankole, southwest Uganda	1,525 (5,000)	Juvenile female	Nov 1903	D. Radcliff
<i>C. m. doggetti</i>	ZD.1929.5.14.17	Manzira (=Minziro) Forest, Katera, Masaka, southwest Uganda	1,160 (3,800)	Adult female	3 Nov 1928	C. R. S. Pitman
<i>C. m. doggetti</i>	ZD.1930.8.1.19	Manzira (=Minziro) Forest, Katera, Masaka, southwest Uganda	1,160 (3,800)	Adult male	10 Aug 1929	C. R. S. Pitman
<i>C. m. doggetti</i>	ZD.1930.8.1.20	Manzira (=Minziro) Forest, Katera, Masaka, southwest Uganda	1,160 (3,800)	Adult male	10 Aug 1929	C. R. S. Pitman
<i>C. m. doggetti</i>	ZD.1930.8.1.21	Manzira (=Minziro) Forest, Katera, Masaka, southwest Uganda	1,160 (3,800)	Adult male	13 Aug 1929	C. R. S. Pitman
<i>C. m. doggetti</i>	ZD.1930.12.1.7	Mt. Sabinio, extreme southwest Uganda	2,740-3,050 (9,000-10,000)	Adult male	Oct 1929	C. R. S. Pitman
<i>C. m. doggetti</i>	ZD.1933.5.17.3	Missenyi, extreme northwest Tanzania	1,150-1,250 (3,773-4,101)	Adult (?male)	15 Jul 1932	R. H. D. Arundell
<i>C. m. doggetti</i>	ZD.1933.5.17.4	Busenya Forest, Missenyi, extreme northwest Tanzania	1,150-1,250 (3,773-4,101)	Adult (?male)	Jul 1932	R. H. D. Arundell
<i>C. m. opisthostictus</i>	ZD.1894.3.8.22 lectotype	L. Mweru, Zambia	c. 1,000 (3,280)	Adult male	?	A. A. Sharpe
<i>C. m. opisthostictus</i>	ZD.1892.2.6.2 paralectotype	L. Mweru, Zambia	c. 1,000 (3,280)	Adult male	?	A. A. Sharpe
<i>C. m. kolbi</i> × <i>C. m. albogularis</i> hybrid	ZD.1972.92	Captive bred. Tigoni, central south Kenya	2,100 (8,690)	Subadult male	31 Oct 1968	C. P. Booth (see Booth 1968)
<i>C. m. kolbi</i> × <i>C. m. albogularis</i> hybrid	ZD.1972.93	Captive bred. Tigoni, central south Kenya	2,100 (8,690)	Subadult male	19 Oct 1968	C. P. Booth (see Booth 1968)
<i>C. m. kolbi</i> × <i>C. m. albogularis</i> hybrid	ZD.1972.94	Captive bred. Tigoni, central south Kenya	2,100 (8,690)	Subadult male	19 Oct 1968	C. P. Booth (see Booth 1968)

<i>C. m. kolbi</i> × <i>C. m. albogularis</i> hybrid	ZD.1972.95	Captive bred. Tigoni, central south Kenya	2,100 (8,690)	Infant female	29 Oct 1968	C. P. Booth (see Booth 1968)
The National Museums of Kenya, Nairobi, Kenya						
<i>C. m. kolbi</i>	151	Ngong Forest, central south Kenya	1,829 (6,000)	Adult male	Jun 1939	Coryndon Memorial Museum
<i>C. m. kolbi</i>	152	Nairobi, central south Kenya	1,676 (5,500)	Adult male	1 May 1918	Coryndon Memorial Museum
<i>C. m. kolbi</i>	1907	Nairobi, central south Kenya	1,676 (5,500)	Adult female	17 Feb 1944	?
<i>C. m. kolbi</i>	8614	Uplands Forest, Mt. Kenya, central Kenya	2,438 (8,000)	Adult male	28 Mar 1962	C. P. Booth
<i>C. m. kolbi</i>	8617	Muguga, central south Kenya	2,134 (7,000)	Subadult male	18 Sep 1961	C. P. Booth
<i>C. m. albotorquatus</i>	6003	Sokoke Forest, central east Kenya	c. 100 (328)	Adult male	23 Apr 1958	J. G. Williams
<i>C. m. albotorquatus</i>	6094	Sokoke Forest, central east Kenya	c. 100 (328)	Adult male	20 Apr 1959	J. G. Williams
<i>C. m. albogularis</i>	153	Chyulu Hills, southeast Kenya	2,134 (7,000)	Adult male	20 Jun 1938	Coryndon Memorial Museum
<i>C. m. albogularis</i>	154	Chyulu Hills, southeast Kenya	2,134 (7,000)	Adult female	Jun 1938	CMM Expedition
<i>C. m. albogularis</i>	6002	Voi Forest, Tsavo NP, southeast Kenya	559 (1,834)	Adult female	1 Jun 1958	J. D. L. Fleetwood
<i>C. m. albogularis</i>	8616	Mrima Hill, southeast Kenya	61 (200)	Adult male	18 Sep 1959	C. P. Booth
<i>C. m. albogularis</i>	8619	Mrima Hill, southeast Kenya	274 (900)	Young adult male	17 Sep 1959	C. P. Booth
<i>C. m. albogularis</i>	8621	Mrima Hill, southeast Kenya	274 (900)	Adult female	17 Sep 1959	C. P. Booth
<i>C. m. albogularis</i>	8622	Chwaka, Zanzibar Island, Indian Ocean, east Tanzania	0 (0)	Adult female	2 Dec 1959	C. P. Booth
<i>C. m. albogularis</i>	MR3	Mrima Hill, southeast Kenya	274 (900)	Adult female	16 Sep 1959	C. P. Booth
<i>C. m. moloneyi</i>	8525	Kisa, L. Rukwa, southwest Tanzania	800 (2,625)	Adult	20 Aug 1955	I. A. D. Robertson
<i>C. m. stuhlmanni</i>	8602	Kipkabus, Eldoret, southwest Kenya	2,470 (8,104)	Adult male	20 Nov 1959	C. P. Booth
<i>C. m. stuhlmanni</i>	8605	Kaimosi, southwest Kenya	1,524 (5,000)	Adult female	10 Oct 1962	C. P. Booth
<i>C. m. stuhlmanni</i>	8606	Kipkabus, Eldoret, southwest Kenya	2,438 (8,000)	Adult female	20 Nov 1959	C. P. Booth
<i>C. m. stuhlmanni</i>	8607	Kibale Forest, Fort Portal, southwest Uganda	1,524 (5,000)	Adult male	4 Oct 1964	C. P. Booth
<i>C. m. stuhlmanni</i>	8608	Kiptagat Forest, Mt. Elgon, southwest Kenya	2,743 (9,000)	Adult male	23 Jun 1964	C. P. Booth
<i>C. m. stuhlmanni</i>	8611	Rotik, Sotik, southwest Kenya	2,071 (6,800)	Adult female	16 Dec 1961	C. P. Booth
Royal Museum for Central Africa, Tervuren, Belgium						
<i>C. m. stuhlmanni</i>	RG 4152 B holotype <i>elgonis</i>	Mt. Elgon, southwest Kenya	?	Adult male?	Pre-1919	L. Bayer
<i>C. m. stuhlmanni</i>	RG 4153 B	Mt. Elgon, southwest Kenya	?	Adult female?	?	L. Bayer
<i>C. m. stuhlmanni</i>	RG 12736	Mt. Elgon, southwest Kenya	?	Adult male	30 Apr 1926	Granvik
<i>C. m. stuhlmanni</i>	RG 11932	Kalonge, Kivu Ruwenzori (Burgeon), central east DRC	?	Adult male	?	?

<i>C. m. doggetti</i>	RG 23015	Lujwigira Valley, Buhanga Ndara, northwest Rwanda	?	Adult male	1 Apr 1954	J. Hiernaux
<i>C. m. doggetti</i>	RG 26.170	Mikenge, central east DRC	?	Adult male	17 Apr 1957	A. Prigogine
<i>C. m. kandti</i>	RG 3429 holotype <i>insignis</i>	“Congo Forest”, DRC	?	Adult	Jul 1914	Zoo Antwerpen
<i>C. m. opisthostictus</i>	RG 1252	Kitangala, Katanga, southeast DRC	?	Subadult female	4 Sep 1912	R. B. Sharpe
<i>C. m. opisthostictus</i>	RG 9906	Lukonzolwa, extreme southeast DRC	?	Adult male	21 Aug 1929	R. P. Pyckhout
<i>C. m. opisthostictus</i>	RG 14396	Ludonzolwa, extreme southeast DRC	?	Infant	22 Feb 1938	R. P. Tempels
<i>C. m. opisthostictus</i>	RG 14812	Kilwis, extreme southeast DRC	?	Adult male	25 Sep 1938	R. P. Tempels
<i>C. m. opisthostictus</i>	RG 15335	Kanzeze, Katanga, southeast DRC	?	Adult	3 Jun 1939	R. P. Tempels
<i>C. m. opisthostictus</i> × <i>C. m. heymansi</i> hybrid	RG 5344	Piana (Kasai), southwest DRC	?	Adult	?	de Macar
<i>C. m. opisthostictus</i> × <i>C. m. heymansi</i> hybrid	RG 5345	Kasai, southwest DRC	?	Adult	?	de Macar
<i>C. m. opisthostictus</i> × <i>C. m. heymansi</i> hybrid	RG 5871	Piana (Kasai), southwest DRC	?	Adult female?	1 Nov 1921	J. Ghesquière
American Museum of Natural History, New York, USA						
Intermediate between <i>C. m. albogularis</i> and <i>C. m. stuhlmanni</i>	M-161108*	40 km east of Ngorongoro Crater, central north Tanzania	1,100 (3,600)	Adult male	28 Oct 1946	T. D. Carter
Intermediate between <i>C. m. albogularis</i> and <i>C. m. stuhlmanni</i>	M-161109*	40 km east of Ngorongoro Crater, central north Tanzania	1,100 (3,600)	Adult male	29 Oct 1946	T. D. Carter
Intermediate between <i>C. m. albogularis</i> and <i>C. m. stuhlmanni</i>	M-161111*	Mto wa Mbu, central north Tanzania	975 (3,200)	Adult male	25 Nov 1946	T. D. Carter
Intermediate between <i>C. m. albogularis</i> and <i>C. m. stuhlmanni</i>	M-161112*	Mto wa Mbu, central north Tanzania	975 (3,200)	Adult male	25 Nov 1946	T. D. Carter
Intermediate between <i>C. m. albogularis</i> and <i>C. m. stuhlmanni</i>	M-161113*	Mto wa Mbu, central north Tanzania	975 (3,200)	Subadult female	25 Nov 1946	T. D. Carter
Intermediate between <i>C. m. albogularis</i> and <i>C. m. stuhlmanni</i>	M-161114*	Mto wa Mbu, central north Tanzania	975 (3,200)	Adult female	26 Nov 1946	T. D. Carter

Appendix III

Visual comparison of the pelage coloration and pattern of the six Manyara *Cercopithecus mitis* specimens at the American Museum of Natural History. Specimens M-161108, M-161109, M-161111, and M-161112 are adult males. Specimen M-16113 is a subadult female. Specimen M-16114 is an adult female. Note the low level of variation among these six specimens. Courtesy of the Trustees of the American Museum of Natural History, New York. Photographs by Sergi López-Torres.





Appendix IV

Standard field body measurements for seven adult and two subadult Manyara monkeys *Cercopithecus mitis manyaraensis*. Of the 17 adult specimens known to be in museums, these are the only seven for which there are body measurements from fresh specimens (see Table 6).

Specimen	Sex	Adult or sub-adult	Total length (mm)	Head-body length (mm)	Tail length (mm)	Hind-foot length (mm)	Fore-foot length (mm)	Ear length (mm)	Weight (g)
M-161108 (AMNH)	M	Adult	1340	555**	785	170	-	-	7711
M-161109 (AMNH)	M	Adult	1242	482**	760	164	-	-	7031
M-161111 (AMNH)	M	Adult	1251	561**	690	154	-	-	-
M-161112 (AMNH)	M	Adult	1209	489**	720	155	-	-	-
ZD.1972.90 (NHM)	M	Adult	1411*	606	805	165	114	37	7930
M-161114 (AMNH)	F	Adult	1167	473**	694	137	-	-	-
ZD.1937.11.8.1 (NHM)	F	Adult	1110*	440	670	129	-	34	-
M-161113 (AMNH)	F	Sub-adult	1000	380**	620	129	-	-	3629
ZD.1972.89 (NHM)	F	Sub-adult	1060*	438	622	130	90	33	2890

* Measurement not taken by collector. Calculated by authors: head-body length + tail length = total length.

** Measurement not taken by collector. Calculated by authors: total length - tail length = head-body length.

Appendix V

Summary of where in the Lake Manyara Study Area the four species of primate that are sympatric with Manyara monkey *Cercopithecus mitis manyaraensis* were encountered during this study. The number of encounters is also presented.

Olive baboon *Papio anubis* (Lesson, 1827) (36 groups encountered): Ngorongoro CA (including Empakaai Crater), L. Manyara NP, Mt. Hanang NFR, and sites in between.

Hilgert's vervet *Chlorocebus pygerythrus hilgerti* (Neumann, 1902) (14 groups encountered): Ngorongoro CA, L. Manyara NP, Mt. Hanang NFR.

Uganda lesser galago *Galago senegalensis sotikae* Hollister, 1920 (9 individuals encountered): L. Manyara NP.

Pangani small-eared galago *Otolemur garnettii panganiensis* Matschie, 1906: (10 individuals encountered): Ngorongoro CA, L. Manyara NP, Mt. Hanang NFR.