COMPARATIVE MORPHOMETRIC STUDY OF PROBOSCIDEAN DENTITION FROM THE APAK MEMBER OF THE NACHUKUI FORMATION AT LOTHAGAM, KENYA.

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MEB/00502/19

A RESEARCH THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENT FOR THE AWARD OF A MASTER'S DEGREE IN HUMAN EVOLUTIONARY BIOLOGY OFTURKANA UNIVERSITY COLLEGE (A CONSTITUENT COLLEGE OF MASINDE MULIRO UNIVERSITY OF SCIENCE AND TECHNOLOGY).

August 2022

DECLARATION AND CERTIFICATION

DECLARATION BY THE STUDENT

This research is my original work and has not been presented for a degree in another university or award.

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APPROVAL BY THE UNIVERSITY SUPERVISORS

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DEDICATION

I dedicate this work to my mum Anastacia Beth Mbatha, my brother Benjamin Wambua, and my beloved children (Eric Muoki, Simon Mumo, and Brian Nyaga) for their unwavering love, encouragement, and patience.

ACKNOWLEDGMENT

I wish to thank my supervisors, Dr. Bill Sanders of the Museum of Paleontology, University of Michigan, and my University supervisor, Dr. Peter Edome Akwee, for their constant guidance, invaluable support, and positive criticism that shaped my progress throughout this study.

Very special thanks would go to Turkana Basin Institute for funding my study and to the Director-General National Museums of Kenya for offering me a study leave to accomplish all my classwork. I also wish to thank Dr. Manthi, Dr. Kibii, Dr. Emma Mbua, my colleagues, my fellow student Emmanuel, and family members whose encouragement and support provided the much-needed conducive environment for the study.

This thesis success and completion is a product acquired from the support and contribution of my Academic advisers, family members, and friends. I am highly indebted to all my supervisors and academic professors for their positive criticism and academic input which shaped this thesis. They include Dr. Bill Sanders of Michigan University, Prof. Nengo of Stony Brooke University and Turkana Basin Institute, Prof. Princehouse of Case Western Reserve University, and Dr. Peter Edome Akwee of Turkana University College, for their positive criticism and academic input, which shaped this thesis. I also wish to thank Madam Ann Nengo for her invaluable training and the constant guidance in good writing and editing. My colleagues in the Earth Science Department and the entire team of Turkana Basin Institute thank you so much for your great support and encouragement. You were, all indeed a blessing whenever I need your help. Lastly, to all my lecturers, I appreciate you a lot for mentoring and teaching me to be suitable in the professional world.

ABSTRACT

The early Pliocene interval of the Apak Member at Lothagam, Kenya, documents significant faunal turnover. During this time, wooded savannas and savanna woodlands expanded in eastern Africa, and elephants consequently evolved to better adapt to grazing. It is also the time of the first appearance of the hominin *Australopithecus*, many modern antelope tribes, new horses, hippos, and pigs. Proboscidean species previously identified from the Apak Member include *Deinotherium bozasi*, *Anancus kenyensis, Stegotetrabelodon orbus,* cf. *Elephas ekorensis*? aff. *Loxodonta*, *Loxodonta exoptata*, and several unidentified elephantids. This study describes new proboscidean specimens and compiles a database of proboscideans from the Apak Member at Lothagam. The study focuses on measurements and morphological descriptions of 14 new and 12 previously studied specimens housed at the National Museums of Kenya. Essential features studied include relative height of the crown (hypsodonty index), which is important for grazing animals, and number of molar plates, which increase in more advanced proboscideans. The study further compares the new database, with that of late Miocene Lothagam proboscideans and proboscidean assemblages from nearby sites of similar age, particularly those from other sites in or near Turkana Basin including Kanapoi, Ileret, and South Turkwel. The objectives were to increase our knowledge of the transition from archaic to more advanced proboscideans in Africa and proboscidean cohorts' role in shaping ecosystem changes. The results meaningfully revise upwards, the taxonomic composition of proboscideans in the Apak Member, and reveal a complex relay of primitive to more derived elephants during the early Pliocene, that documents the adaptive response to increased competition among mammals for grazing resources.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABBREVIATIONS AND ACRONYMS

Dental abbreviations

ET, enamel thickness.

dp/dP = lower/ upper deciduous premolar, for example, dp4 is a lower fourth deciduous permanent premolar.

H = tooth crown height.

W, tooth crown width (including dentine/cementum).

HI, hypsodonty index (H multiplied by 100 and divided by W), in proboscideans, indicates the relative crown height.

LF = lamellar frequency (number of plates per 100mm).

M/m means upper/lower molar; for example, M3 is an upper third molar.

R or rt = right.

L or lt = left.

P/p, upper/ lower permanent premolar. For example, p3 is a lower third permanent premolar.

x, posterior or anterior cingulum or cingulid, like x4x, indicates a molar tooth with four (4) loph(id)s.

+, either on the posterior or anterior cingulids, indicates missing dental morphology (Sanders et al., 2020).

Abbreviations

KNM, National Museums of Kenya; **LT**, specimens from Lothagam, Kenya; **Mb,** geological Member; **Mya,** million years ago; **Fm,** geological Formation.

CHAPTER ONE

1.0 INTRODUCTION

1.1 Background of the study

Proboscidea is a mammalian order which comprises the elephants and their extinct relatives. All members of this order have a trunk or proboscis that they use to grab food and water. Proboscideans are represented in modern Africa by the savannah elephant *Loxodonta africana* and forest elephants *Loxodonta cyclotis* (Harris et al., 2010; Sander, 2020). The first true proboscideans evolved and diversified in Africa in the Paleogene (65.5 to 23 Mya). *Phosphatherium escuilliei* is the earliest recognized proboscidean from the late Paleogene (58 Mya) of Morocco (Sanders et al., 2010, 2021; Uno et al., 2020).

Early proboscidean species starting from the earliest include *Phosphatherium, Daouitherium, Moeritherium, Numidotherium,* and *Barytherium,* whereas Elephantiformes are represented by Palaeomastodontidae and Elephantimorpha (Elephantida: Gomphotheriidae (extinct), Stegodontidae (extinct), and Elephantidae; plus, Mammutida: Mammutidae (extinct) (Sanders, 2020; Uno et al., 2020). Deinotherioidea is a group of archaic proboscideans possibly derived from the early plesielephantiform proboscideans that arose in the Oligocene and persisted in Africa until the end of the Early Pleistocene (Harris, 1978; Sanders et al., 2010). Deinotherium had a fully functional trunk and a downward recurving tusks in the lower jaw, a trait only present to them and not in other proboscideans. This unique trait was thought to be used for mate recognition and for manipulation of their short proboscis. (Uno et al., 2020; Sanders, 2020; Sanders et al., 2021).

Elephants (Elephantidae) evolved in Africa during the late Miocene from tetralophodont ancestors with primitive dental characters such as brachydonty and molars with few loph(id)s and rounded cusps rather than a plates – transverse ridges or lamellae that characterize elephants (Harris et al., 2003; Sanders et al., 2021). The emergence of Elephantidae from tetralophodont Gomphotheriidae indicates a major adaptive shift in chewing strategies. (Lister, 2013; Sanders, 2020). These changes led to increased expansion of the Elephantidae, which partly led to the replacement of most gomphothere groups, and became the dominant herbivore during the Pleistocene. Some of the distinctive features of elephantiform proboscideans include large, projecting tusks, enormous pneumatized cranial with retracted nasal apertures (associated with trunks), massive bodies, and graviportal postcranial adaptations (Sanders et al. 2012; Sanders, 2020).

In Kenya, elephant species have been found from the late Miocene (about 7.5 Ma) to the present, particularly in sites in or near the greater Turkana Basin, such as Koobi Fora, Ileret, South Turkwel, Kanapoi, the Tugen Hills, and Lothagam (Harris et al., 2003; Uno et al., 2020). The family is represented in Kenya's fossil record by at least five different genera: *Stegotetrabelodon* (extinct), *Primelephas* (extinct), *Mammuthus* (extinct), *Loxodonta* (African elephants), and *Elepha*s (represented today by the Asian elephant) (Sanders et al., 2021). The Lothagam sequence was subdivided into three units by Behrensmeyer (1976) as follows: Lothagam 1 & 2 are both Miocene age, and Lothagam 3 is classified as Pliocene. The Apak Member of the Nachukui Formation of Lothagam 3 provides a greater diversity of the fossil proboscideans, including more derived species such as *Loxodonta adaurora*, lacking in other units (Maglio, 1973; Behrensmeyer et al., 1982; Sanders et al., 2021).

Between 1963 – 1968, Bryan Patterson initiated a series of Harvard University expeditions at Kanapoi and Lothagam and discovered over 500 fossil specimens, including most of Maglio's proboscidean fossil materials (Sanders, 2020). In 1980, Meave and Richard Leakey and the Koobi Fora Research project (KFRP) collected significant Mio – Pleistocene vertebrate assemblages at Lothagam. Fieldwork at Lothagam from 1989 to 1993 by the National Museums of Kenya expedition yielded additional new elephant specimens and taxa, especially from the Apak Member of the Nachukui Formation. Constituent species have been said to include *Deinotherium bozasi, Anancus kenyensis, Stegotetrabelodon orbus, Elepha ekorensis, Loxodonta adaurora*, and other two Elephantidae gen. and spp., described as *incertae sedis* A & B (Tassy, 2003; Sanders et al., 2010; Uno et al., 2020).

Stegotetrabelodon orbus is more derived and elephant-like than its North African and Arabian relatives, *S. syrticus* and *S. emiratus.* The earliest elephantine is *Primelephas korotorensis (*formerly *gomphotheroides*), thought to be the ancestral genus of later elephants (*Elephas, Loxodonta*, *and Mammuthus*). *Their dental and cranial character differences distinguish Loxodonta adaurora from Mammuthus africanavus and M. subplanifron*s. It is also among the earliest known members of the *Loxodonta* lineage and was once considered the direct ancestor of African living species of elephants. *Loxodonta adaurora* is now understood to be an evolutionary cousin of *Loxodonta africana* and *Loxodonta cyclotis* (Manthi et al., 2017; Sanders, 2020). *Elephas ekorensis* is more plesiomorphic than *Elepha recki* in its dental and cranial morphology, suggesting it is ancestral to this lineage (Manthi et al., 2017; Sanders, 2020; Sanders et al., 2021).

1.2 Statement of Problem

The early Pliocene interval represented by the Apak Member has been documented as a time of significant faunal turnover represented by many new mammal species that replaced their more archaic late Miocene predecessors (Harris & Leakey, 2003). It is also the time of the first appearance of the hominin genus *Australopithecus*. Hominins are definitely known from the Lothagam sequence by the Apak Member (the australopith mandible KNM-LT 329). The proboscidean fossil sample warrants a more careful study and re-identification, especially given new advances in proboscidean studies.

Properly documenting the transition from archaic to more advanced proboscideans is essential, to understanding faunal turnover and hominin success, as proboscideans are keystone taxa in ecosystems changes. Proboscideans are also responsible for creating more heterogeneous ecosystems where many new mammalian taxa could thrive. Proboscidean species that have been recovered and previously identified from the Apak Member include *Anancus kenyensis*, *Stegotetrabelodon orbus, Elephas* cf. *E. ekorensis,* and *Loxodonta?* aff. *Loxodonta Exoptata,* and *Loxodonta adaurora*. The proboscidean assemblage also includes several unidentified elephantids (Wang et al., 2017; Sanders et al., 2021).

Earlier studies of Lothagam proboscidean by (Maglio, 1970, 1973; Maglio & Rica, 1977; Tassy, 2003; Sanders et al., 2010) indicate that many species were left out and others erroneously described. For example, specimen described by (Maglio, 1973) to be *Loxodonta exoptata*, has turned out to be *Loxodonta cookei*. The other reason why the study was significant was that the Lothagam proboscideans were studied a long time ago, and we now know more about proboscidean's evolution and phylogeny than we did ten and twenty years ago. Therefore, a more careful re-analysis of the proboscideans was crucial for establishing the exact number of proboscideans at Lothagam, especially the Apak Member of the Nachukui Formation, including all their taxonomic identity.

1.3 Purpose of the study

The primary goal of this study was to identify new proboscidean specimens and have a substantial database of these proboscideans, to compare them with older Lothagam proboscidean specimens from the late Miocene, and with proboscideans assemblages from sites of similar age. Particularly, those from other places in or near Turkana Basin (including Kanapoi, Ileret, and South Turkwel) dated about the same period as the Apak Member.

1.3.1 General objective

The main objective of this study was to make a taxonomic study of the entire Apak Member Lothagam proboscidean collection at NMK, which consists mostly of isolated teeth, dated to about 4.2 million years.

1.3.2 Specific objectives

The specific objectives of the study were;

1. To describe and taxonomically assign proboscidean dental specimens from the Apak Member assemblage not previously studied.

2. To reassess the alpha taxonomy of previously described proboscidean dental specimens from the Apak Member of Nachukui Formation.

3. To establish the number and taxonomic identity of proboscideans species at Lothagam, especially from the Apak Member of Nachukui Formation.

1.4 Research questions

To achieve the objectives of this study, the research study seeks to answer the following questions:

1. What is the taxonomic composition of proboscideans species in the Apak Member of the Nachukui Formation at Lothagam?

2. How many species are represented in the current proboscideans sample, especially from the Apak Member of the Nachukui Formation, at Lothagam?

1.5 Justification of the study

Elephants first appeared in Africa in the late Miocene (Sanders, 2020). Numerous fossil found in African Mio-Pliocene sites indicates that, multiple elephant species coexisted during this time period. My research was significant because the temporal interval of the Apak Member was a time of substantial faunal turnover and represents a relay interval in proboscidean evolution when primitive stem elephants were being replaced by more advanced elephants that were better adapted morphologically for grazing (Wandelin et al., 2010; Monthe et al., 2017; Sander, 2020).

It is a significant time in African faunal evolution, as our *Australopithecine* ancestors first arose during that interval. Possibly, benefiting from their adaptations to explore heterogenous environments that were being transformed in parts by the activities of multiple sympatric proboscidean taxa that were opening up landscapes in a manner advantageous to other grazing mammals such as bovids, suids, hippos, rhino, horses, and bipedal hominins (Sanders et al., 2021). Additionally, the Apak proboscideans collections have never been fully studied. We also know more now about proboscidean evolution than we did in the past. The main objective of this study was to provide information that could improve our understanding of whether evolutionary changes in elephants are in phase with environmental changes at Lothagam in the transition from the late Miocene and early Pliocene. (Sanders et al., 2021).

1.6 Scope of the study

The study was focused on materials from Lothagam, especially the Apak Member of the Nachukui Formation. The faunal assemblage of Lothagam is very rich and diverse. The Apak Member provides a greater diversity of proboscideans fossils, including a more derived species, *Loxodonta adaurora*. These proboscidean species are hence making the site necessary for paleontological field research. Older Lothagam proboscideans from the Late Miocene and proboscideans assemblages from similar age sites, especially in the Turkana Basin, were also included in the study for comparative purposes.

1.7 Limitation of the study

The study's first limitation was the inability to locate the partial skull of *Loxodonta adaurora* KNM-LT 353 at the National Museums of Kenya paleontology lab. *Loxodonta adaurora* is one of derived species collected in Lothagam, especially in the Apak Member of Lothagam 3. Specimen KNM – LT 353, (Maglio, 1973) had erroneously been listed as the specimen in his publication as KNM – LT 383. Therefore, locating this specimen was an uphill task. The movement of specimens from known shelf number and failing to update their new location, was also a critical limiting factor.

CHAPTER TWO

2.0 LITERATURE REVIEW

2.1 Introduction

This section describes different proboscidean species found at the Apak Member of Lothagam, Kenya, starting from the most primitive species to the most derived ones. The description of the proboscideans includes their origins, physical characteristics, and identified species with wrong descriptions. Many of the Plio – Pleistocene sites in northern Kenya have produced numerous fossil proboscidean species (Maglio, 1970; Sanders, 2020), including Kanapoi, Lothagam, the Tugen Hills, and Ekora. The proboscidean fossils include *Deinotherium bozasi, Anancus spp.; Loxodonta adaurora; Loxodonta cookie; Mammuthus subplanifrons; Elephas ekorensis; Elephas nawataensis; Elephas* (or *Palaeoloxodon*) *recki; Stegotetrabeledon orbus,* and *Primelephas gomphotheroides* now *korotorensis* (Sanders, 2020).

Researchers, including (Maglio, 1970, 1973; Sanders, 2020; Sanders et al., 2021), described the dental characteristics of elephants as comprised of molars formed of loph(id)s/plates, or lamellae, which are held together by dentine/cementum. Studies (Sanders et al., 2021) also indicate that, within the Order~~,~~ Proboscidea, molars of elephants are more advanced/derived. Their ancestral histories involved an evolutionary transformation from gomphotheriid – type molars comprised of conelets, cusps, and conules arranged in complementary half–plate/loph(id)s (Maglio, 1970, 1973; Sanders et al., 2010; Sanders, 2017, 2020).

The late Miocene-early Pliocene period is characterized by features such as the disappearance of gomphotheriid lineages that seem to have started disappearing from Africa; due to ecological/environmental change and competition with elephants. These changes evolved substantial and advanced morphological innovations that provided them with more effective masticatory adaptations to new resources and better life histories (Sanders et al., 2010).

The isotopic analysis of the elephant's dental characteristics indicates that some elephant populations fed mostly on substantial amounts of C4 grasses in their diets (Kingston, 1999; Cerling et al., 1999, 2003; Uno et al., 2011). According to (Sanders et al., 2021), the proboscidean dental characteristics were in phase with the ecological and climatic changes in the Plio-Miocene period, especially at the Apak Member of Nachukui Formation at Lothagam Kenya. These ecological changes seem to have favored expansion of partially open grassy woodlands and open savannas (Cerling et al., 1997; Kingston, 1999; Sanders et al., 2020, 2021).

The molar of the primitive elephants has been indicated to have few widely spaced plates, very thick, unfolded enamel, very low crowned (brachyodont), pyramidal bulbous lateral plate profiles, and modest coatings of crown cementum (Maglio, 1973; Sanders et al., 2010, 2021;). Other factors driving evolutionary selection include competition for resources between proboscidean species (including *stegodonts*, *anancine gomphothere*, and elephant species). Coupled with the increasing spread of wooded savannas and C4 grasses throughout the Pliocene period in East Africa (Leakey and Harris, 2003; Sanders et al., 2010; Cerling et al., 2014). These species with greater adaptation to grazing, such as *Loxodonta adaurora*, had high-crowned molars constructed of a more significant number of plates and a thicker covering of cementum; that was more durable against dental attrition associated with feeding on C4 grasses (Sanders et al., 2010; Sanders, 2020). These species were favored during the Pliocene period, represented by the Apak Member.

Primelephas korotorensis seem to have low crowned upper third molars and few plates, (only seven). *Stegotetrabelodon orbus*, as described by (Sanders et al., 2010; Maglio, 1970, 1973), is a late Miocene-early Pliocene stem elephantids characterized by numerous primitive dental features such as retention of lower tusk and P3 -4/p3-4. Including very brachyodont molars with few plates or loph(id)s and very thick enamel molars. Other characteristics include low lamellar frequency, pyramidal plate shape, and weak covering of cementum (Maglio, 1973; Sanders et al., 2010, 2021).

Studies done by (Maglio and Ricca, 1977; Sanders, 2020) indicate that *Loxodonta adaurora* has been the only dominant elephant species in the Turkana basin, including the Apak Member in the early to mid - Pliocene period. Additionally, (Manthi et al., 2017) demonstrated using dental isotopes that *Loxodonta adaurora* was a mixed feeder and a typical grazer that fed mainly on C4 grasses (Uno et al., 2020).

2.1.1 *Deinotherium bozasi*

Deinotheres were the only massive and non – elephantimorph species that survived until the Neogene. After the early Miocene, deinotheres faunal numbers were seen to be limited, meaning that either they were antisocial or lived farther away from depositional settings. They may have had smaller home ranges than elephants (Sanders et al., 2020). Deinotheres are distinguished from other elephant species by their massive bodies, absence of upper tusks, and crested sharp bilophodont teeth (except for M1/m1 and dP4/dp4) retained throughout their life histories and their downward curvature of the mandibular symphysis and lower tusks (Sanders, 2021). Their downward curved lower tusks probably indicated an existence in highly dense environments (Harris, 1978). Additionally, (Sanders et al., 2010) suggested that deinotheres remained browsers of the C3 diet (3-phosphoglycerate) till they disappeared in the early Pleistocene.

2.1.2 *Anancus kenyensis*

This is a late Mio - Pliocene species aged 7.4 to 4.3 million years, as described by (Sanders et al., 2010), found in the Apak Member of the Nachukui Formation. *A. kenyensis* was also discovered in Lothagam, Kenya, at Upper and Lower Nawata Formation localities (Tassy, 2003). *Anancus kenyensis* was also found in the eastern and western side of Kanam, Kenya (Maclnne, 1942; Tassy, 1986), the Lukeino Formation in the Tugen Hills and the Mpesida Beds, Kenya (Tassy, 1986), Manonga Valley, Tanzania (Sanders, 1997), in late Miocene-early Pliocene sites in Ethiopia (Kalb & Mebrate, 1993; Saegusa and Haile-Selassie, 2009), Uganda at Nkondo (Tassy, 1985), and in Chad (Hautier et al., 2009). *Anancus spp*. originated in Eurasia and became prominent in Europe, Africa, and Asia by the late Miocene to early Pleistocene (Tassy, 1985).

There are several African species of *Anancus*: *Anancus kenyensis*, *Anancus petricchii*, *Anancus ultimus, Anancus capensis, and Anancus osiris. Anancus petrochii* is a late Miocene species only found in Sahabi, Libya, though Mackaye, (2001) claims it is present at Toros-Menalla in Chad. *Anancus petrocchii* is characterized by having pentolophodont intermediate molars, with their third molars having six loph(id)s and primitive, simple crowns with very weak anancoidy (Petrocchi, 1943, 1954; Coppens, 1965; Sanders et al., 2021). Their molar teeth are also said to be enormously constructed, with little evidence of accessory conules. A recent study by Sanders, et al., (2021) of unpublished fossils from Sahabi shows that the accessory conules of this species are complex.

A primitive species of *Anancus* at Lothagam was first described by Smart (1976) and later interpreted by (Coppens et al., 1978) as *Anancus kenyensis*. However, (Tassy, 1986) recognized two primitive morphological features of *kenyensis* from Kanam. The primitive *A. kenyensis* in East Africa is well documented, and it has been recorded in Mpesida, Lukeino, Kanam, and

Lothagam (Tassy, 1986). Its advanced successor species, *Anancus ultimus*, has pentalophodont intermediate molars, with an excessively pronounced anancoidy, or offset of half – loph(id)s. Their third molars have six to seven plates, complex dental morphology with higher expression of accessory conules, and finely folded enamel. However, the *petrocchii* morphological description by Tassy, 1996 is confusing because Kanam specimens are more derived than the simple *petrocchii* dental characters (Sanders, 2020). However, (Sanders, 1997) indicates that Sahabi molars are characterized by their large size, reasonably good distribution of accessory conules, and strong anancoidy. According to (Sanders, 1997), their large size sets them apart.

The East African primitive *Anancus* species, as described by (Sanders, 1997; Tassy, 1986; Kalb & Mebrate, 1993), presents simple molars with plesiomorphic characters. These characters include tetralopontodont intermediate molars with unfolded thick enamel, weak anancoidy, and simple occlusal morphology whose posttrite accessory conules are visible in the first anterior plates of the third molars. The molar tooth is characterized by massive and bulbous loph(id)s in the lateral view (Sanders, 2020).

The *Anancus kenyensis* from Kanam, Kenya, indicates simple morphology. Still, with no fifth loph, Apak member, dental characters are distinct and sophisticated but, not as complicated as with *Anancus* molars from Kanapoi, Aterir, Kenya. The dental characters among all Lothagam *Anancus* suggest a similar evolutionary level of *Anancus* in eastern Africa dated at around four and a half million years old, especially in *Anancus kenyensis* (not *Anancus ultimus*).

2.1.3 *Stegotetrabelodon orbus*

This extinct species is found in the late Miocene and early Pliocene beds of Lothagam Hill, Kenya. Other significant stegotetrabelodont localities of a similar age include Sahabi, Libya (Petrochi, 1943, 1954; Graziry, 1987; Sanders, 2008), sites around lake Chad, Adu – Asa, Ethiopia (Kalba & Membrate, 1993; Mackaye, 2001; Saegusa & Haile, 2011), Manonga Valley, Tanzania (Sanders, 1997), and some later Miocene sites in western Kenya such as Narok. *Stegotetrabelodon orbus* has more derived upper molars than *Stegotetrabelodon syrticus*. However, both species display similar plate numbers, six on the upper M3 and seven on the lower m3. Phyletically, *Stegotetrabelodon* is a possible immediate ancestor to *Elephantidae* after *Gomphotheriidae*, and they seem to have retained gomphothere primitive characters, including long mandibular incisors. Still, their molars are more elephant-like than gomphothere–like (Coppens et al., 1978; Sanders et al., 2010; Sanders et al., 2013).

Stegotetrabelodonts, as described by (Maglio, 1973; Sanders et al., 2010) can be identified by the retention of primitive features such as retention of P3 – 4 / p3 – 4 and lower tusks. Other vital features include few plates or loph (id)s, brachyodont or low crowned molars, pyramidal plate shape, thick enamel, weak covering of cementum, and low lamellar frequency (Maglio, 1973; Sanders et al., 2010). The description and measurement of the original proboscidean collection from Lothagam were first published by (Maglio, 1970, 1973; Maglio & Ricca, 1977; Tassy, 1986). However, (Tassy, 1986) noted that specimen KNM - LT 350 elements were erroneously described by (Maglio, 1973) and given wrong species identity.

Tassy's description of the two new specimens collected in 1989 and 1993, KNM - LT 26318 and KNM – LT 26334, was either from the Nawata Formation or Apak Member, which needed to be clarified (Sanders, 2020). Other specimens, such as KNM – LT 355, had the same issue and needed clarification. Tassy noted that specimen KNM – LT 366 was wrongly described as M2, which (Tassy, 2003) indicated was an M3 because the posterior end of the tooth is narrow and has a subdivided root. Additionally, (Tassy, 2003) also noted that the wear pattern was asymmetrical, more pronounced lingually on the first two plates and more pronounced labially on the rear plate.

Other unusual descriptions were also noted in specimen KNM – LT 367. (Maglio, 1973) described specimen KNM – LT 363 from the Apak Member as *Primelephas gomphotheroides* and its element as a partial right M3 and mandibular symphysis. However, (Tassy, 1986) described the molar as *Stegotetrabelodon orbus* and noted that the mandibular symphysis did not belong to the same individual, which was thoroughly checked. The specimen KNM – LT 359 was described as Upper Nawata proboscidean fossil material (Maglio, 1970; Tassy, 1986). However, it belonged to the Apak Member as per the accession register at the National Museums of Kenya.

2.1.4 *Primelephas koroterensis*

This species is characterized by very low-crowned molars with well-developed plates. It has been found in Kenya at Lothagam, the Lukeino Formation in the Baringo Basin (Tassy, 1986), in Chad (Mackaye, 1942), in the Kaiso Beds, Uganda (Tassy, 1995), Ethiopia from Adu – Asa formation of Awash valley (Kalb et al., 1993), and the Manonga – Wembere Formation, Tanzania (Sanders, 1997) in the late Miocene. Over 15 specimens have been grouped to either *Primelephas korotorensis* or *Stegotetrabelodon* without a thorough investigation, especially for the specimen with a field number, 290 - 67 K, which (Maglio, 1973) assumed to be *Primelephas korotorensis*.

The specimen described by both (Maglio, 1973; Tassy, 2003) as Elephantidae gen and sp *incertae Sedis A*, seems to be distinct in its dental morphology, compared to M3(s) of *Primelephas korotensis* and *Stegotetrabelodon orbus* seems. The above exhibited traits belong to an elephantine with a low lamella frequency. The considerable dentine (cementum) also suggests that specimen KNM – LT 23785 is a more derived species. (Maglio, 1970) described specimen *Incertae Sedis B* as having too thin plates associated with *Stegotetrabelodon orbus*. However, it was similar to *Primelephas Korotorensis* despite having a higher lamella frequency. The thinner enamel and high lamella frequency are derived characters related to more advanced species, thus requiring closer analysis of the molar tooth.

2.1.5 *Loxodonta sp.* aff. *L. exoptata*

This is an East African Pliocene elephant species with the best fossil remains found in Tanzania, in the upper Laetolili Beds (Sanders, 2011; Beden, 1987a). Additionally, (Harris et al., 1988; Harris et al., 2003) explained that *Loxodonta exoptata* was also found in Pliocene sites in Kenya at west Turkana and Kanapoi in the Nachukui formation. As per (Sander's, 1997, 2011; Beden's, 1987a) descriptions, specific sites were Tanzania, in the Upper Ndolanya Beds at Laetoli, Ethiopia in the Denen Dora Member of the Hadar Formation, and Uganda at Nyakabingo and Warwire formation in areas of Nkondo and Nyabusosi (Tassy, 1995).

Loxodonta exoptata molars are hypsodont with plates which are more closely spaced than the archaic elephant species, moderately thick enamel, and molar enamel wear similarly to modern *Loxodonta africana* (Dietrich, 1941; Sanders et al., 2021). *Loxodonta exoptata* are distinguished from *Loxodonta adaurora* and *Loxodonta cookei* by having too many plates, greater hypsodonty, higher lamella frequency, thinner enamel, and pronounced medium sinuses than *Loxodonta adaurora* (Sanders, 2020). *Loxodonta exoptata* also appears to have a consistent appearance of anterior and posterior conules in all their molar crowns which wear into loxodont sinuses (<>) (Sanders, 2011; Sanders et al., 2021).

According to (Tassy, 1986), Apak member materials indicate that *Loxodonta* species existed in the Apak Member of the Nachukui Formation. Additionally, the specimens displayed dental characters different from those in Laetoli and Koobi Fora (Beden, 1987b) and those in Uganda and Lukeino (Tassy, 1994). The Apak Member materials as (Maglio, 1970, 1973) described it, and (Tassy, 1996) included specimen KNM – LT 23786, posterior m3; KNM – LT 23794, Rt. M3 fragment, and KNM – LT 26321, anterior part, Rt. M3. (Tassy's, 1986) description appeared to be different from those specimens described by Maglio (1970, 1973). Additionally, they posed characteristics identified with *Loxodonta* species, suggesting that Apak Member specimens represented two ancestral species of the extant elephant genera *Elephas* and *Loxodonta* between 4.0 and 5.0 million years ago (Harris et al., 2010; Gheerbrat et al., 2010).

2.1.6 *Loxodonta adaurora*

This is an extinct elephant species only found in Africa during the Pliocene (Sanders et al., 2021). *Loxodonta adaurora* belonged to the genus *Loxodonta* and was previously presumed to be the ancestral species to extant African elephants. However, studies done by various researchers (Sanders, 2011) suggest that *Loxodonta african*a evolved from *Loxodonta exoptata* (Uno, et al., 2020). Strong central posterior and anterior accessory conules in their molar crowns can identify the main *Loxodonta* lineage, forming median sinuses (<>) in wear. The extant or modern elephant *Loxodonta africana* and *Loxodonta cyclotis*, the extinct Pliocene species of *Loxodonta exoptata*, and *Loxodonta cookei* can also be recognized by these similar traits (Sanders, 2004). *Loxodonta adaurora* lacks the development of median sinuses but exhibits strong anterior and posterior accessory conules in the midline of its molar crowns (Sanders, 2020; Sanders et al., 2021).

Other distinctive features that characterize *Loxodonta adaurora* include a more significant number of plates, u – shaped transverse valleys, and corresponding parallel-sided plates, especially in the lateral view. (Maglio, 1973; Sanders et al., 2010) described *Loxodonta* *adaurora* as having greater crown height, thicker distribution of cementum on molar crowns, and a higher lamellar frequency (Sanders, 2020). The species' cranium is high, anteroposteriorly compressed, and its mandible has a much shorter symphysis than in *Stegotetrabelodonts* and lacks lower tusks (Sanders, 2020; Sanders et al., 2021).

2.1.7 *Elephas ekorensis* (Maglio, 1970)

This is the earliest species recognized in the genus *Elephas* at East African sites aged 5.3 to 3.6 million years ago (Uno et al., 2020; Sanders, 2020). The extinct species has two lineages, one "dead-end lineage" of Afro - Eurasia and an Asian lineage that evolved into extant Asian elephants (Uno et al., 2020). *Elephas ekorensis* is the putative ancestor to *Elephas iolensis* and *Elephas recki* (Coppens et al., 1978; Leakey et al., 2003).

According to (Tassy, 1986), the species is represented in the Apak member by specimen KNM – LT 23795 which is a partial Rt. M1 and KNM – LT 26320 which represents a hemi – mandible with dP, and m1. These specimen presents more derived traits and are closer to the Pliocene elephantine of about 4.2 million years ago. Such features include more closely spaced taller plates with cusps less conical and more compressed anteroposteriorly. The specimen description by (Maglio, 1973) indicates that, the Apak Member specimens present primitive traits related to *Elephas ekorensis* and that (Tassy, 1986) attributes these differences to be a primitive evolutionary stage of the Apak materials which are older than 4.2 million years.

2.2 Summary and gaps in the literature

The fossil record indicates that multiple elephant species must have coexisted due to numerous fossil finds in many African Mio – Pliocene sites (Leakey et al., 2003; Shoshani et al., 2006; Sanders, 2020). Some elephant species discovered in these Mio – Pleistocene sites include

Stegotetrabelodon spp, Primelephas gomphotheroides (now *korotorensis*), and anancine gomphotheres, *Loxodonta spp,* among other proboscidean species (Sanders et al., 2010).

Evolutionary changes in early elephants have been recorded in their dental development, particularly the plates' formation in molars and the cranial development that enhanced a fore-aft horizontal shearing form of mastication as described by (Maglio, 1972). However, earlier elephants indicate primitive characters compared to derived species, especially in their dental characteristics. Branchyodont molars characterize the archaic species as indicated by (Sanders, 2020). Other primitive features include; a limited number of plates, thicker enamel, and broad plate spacing, which was later phased out by the evolution of gnathodental adaptations for grazing, as suggested by (Lister, 2013).

A review of proboscidean fossil materials from Lothagam confirms the coexistence of more elephant species in the Apak Member of the Nachukui Formation than was earlier anticipated. The fieldwork from 1989 to 1993 by the National Museums of Kenya expedition team, led by Meave Leakey, suggested the presence of *Loxodonta exoptata, Elephas ekorensis, Anancus kenyensis, Stegotetrabelodon orbus, Loxodonta adaurora*, and *Primelepha korotorensis*. However, earlier studies at the site appeared to have left out some specimens for example collection done between 1980 to 1993 at the Apak Member. While others such as specimen KNM – LT 353, KNM – LT 23340 among other specimens were erroneously described. The current research benefitted from the abundance of data for analysis and comparison from the '89 and '93 field seasons.

Some of the literature reviews have highlighted gaps which include wrong preliminary descriptions produced before adequate comparative data was available, leading to misidentification of proboscidean species by earlier researchers at the site (Sander, 2020, 2021;

Uno et al., 2020). Additionally, (Tassy, 1986), on the other hand, confirmed that some proboscidean species at Lothagam, especially in the Apak Member, had been erroneously described by (Maglio, 1970, 1973). This has resulted in species misidentification. Specimens described by (Maglio, 1970, 1973; Maglio and Ricca, 1977; Tassy, 1986) from Lothagam, Apak Member of the Nachukui formation included; *Anancus kenyensis*, *Stegotetrabelodon orbus, Elephas ekorensis,* and *Loxodonta exoptata*, as well as Elephantidae gen and spp, described as *Incertae sedis* A & B. About eleven (11) essential proboscidean specimens had been left out, by earlier researchers describing the Apak Member fossil materials. This study also indicated the existence of *Loxodonta adaurora,* an extinct species only found in Africa during Pliocene (4.2 Mya), and possibly the presence of *Loxodonta cookie* from the late Miocene – early Pliocene of eastern and southern Africa.

2.3 Theoretical Framework

This research was guided by Charles Darwin and Alfred Russell Wallace's principle of natural selection (REF) (Lister, 2013). This theory attempts to explain the origin and evolutionary histories of different species. The principle predicts that an organism's anatomical characteristics, including dental characters, are shaped by the traits' survival advantage in a given environment. Any change in climate affects individual survival in an ecosystem, and only the best-adapted individuals can survive and reproduce (Sanders et al., 2020). The differences in elephant dental characters represent their evolutionary changes (Shoshani et al., 2006; Sanders, 2020).

The expansion of Elephantidae and the replacement of most archaic proboscidean species was due to a major adaptive shift in chewing strategies among different elephant species (Lister, 2013; Sanders et al., 2020). Therefore, the Pliocene interval of the Apak Member is critical in documenting the transition of proboscidean species from archaic to more advanced proboscideans due to their greater diversity in the fossil record.

Evolution of modern elephants

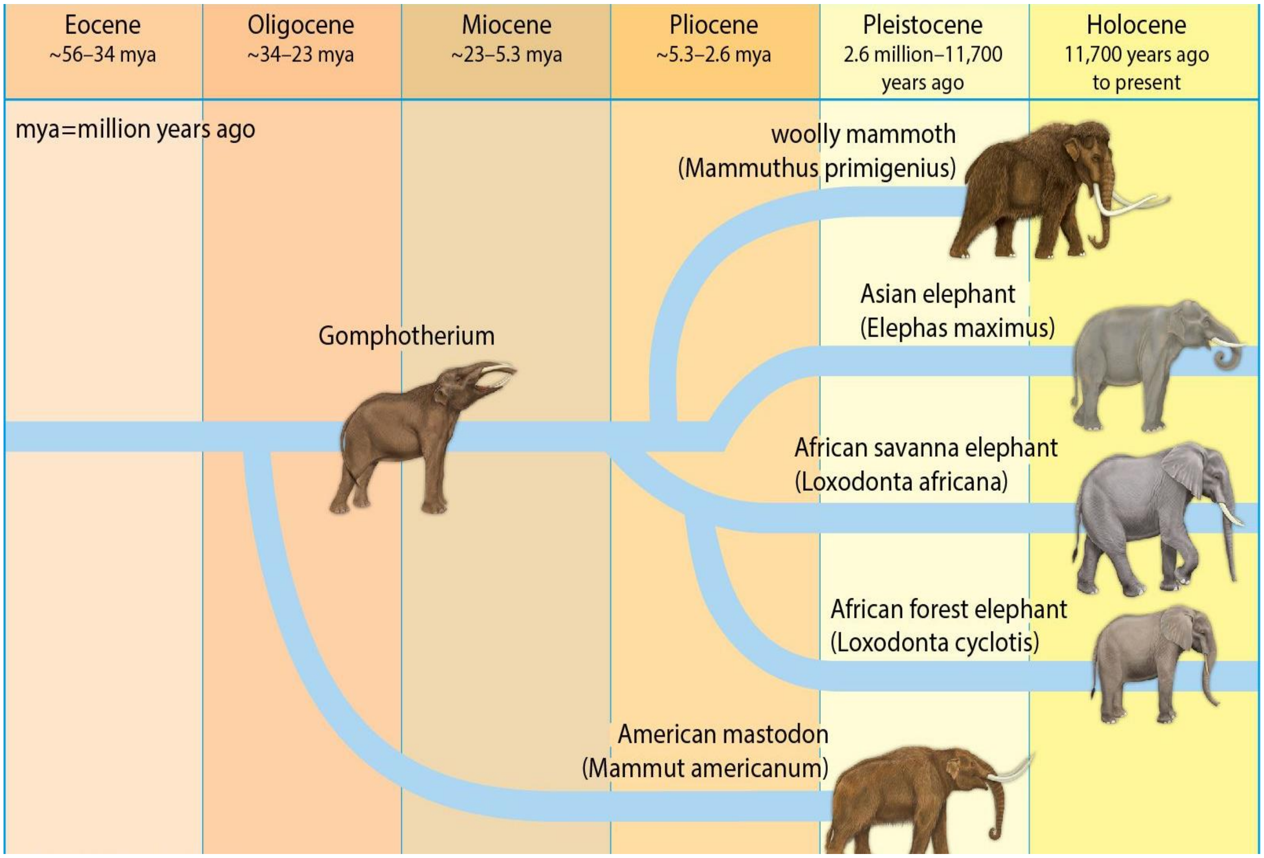

Image source: *Encyclopædia Britannica, Inc.*

CHAPTER THREE

3.0 METHODS AND MATERIALS

3.1 Introduction

This section includes materials, morphometric procedures, study area, and a description of the research design. The section also described the data techniques and analysis and the ethical issues involved.

3.2 Research design

This section used both qualitative and quantitative paleontological field methods, where measurements and descriptions of the proboscidean dental characters were done to identify different proboscidean species. The techniques involved in describing different proboscidean species included estimation such as degree of enamel folding, enamel thickness, hypsodont index, and expression of accessory conules, among other items (Wang et al., 2017).

3.3 Study area

The present study was carried out in Lothagam Hill, which includes Nawata, both Upper and Lower Beds, and the Apak Member of the Nachukui Formation where the study materials were collected. This site is situated at 36^0 04'E and 2^0, 53' N, and 40 miles North of Kanapoi, 3 miles southwest of Kerio delta on the southwest side of Lake Turkana, Turkana County, Kenya (Fig. 3.1 to 3.5). The faunal assemblage at Lothagam is rich and diverse, and the region is characterized by deltaic sediments separated by fine-grained lake beds. The large majority of fossils are late Miocene in age. The vast number of fossil taxa at Lothagam includes fish, reptiles, and mammals (such as *Cercopithecidae, Hominidae, Viverridae, Hyaenidae, Felidae, Machairodontinae, Deinotheriidae, Gomphotheriidae, Elephantidae, Orycteropodidae,* *Sciuridae, Thryonomydae, Hystricidae, Cricetidae,* and *Muridae* (Maglio, 1970, 1973; Sanders et al., 2021).

The fossil site of Lothagam (Turkana Basin, Kenya) provides the richest sequence for studying late Miocene taxonomic turnover and ecological structure in eastern African fossil mammals. Lothagam exposes both Miocene and Plio-Pleistocene sediments (Fig. 3.2 & 3.3), these being the Nawata and Nachukui Formations, respectively. The Nawata Formation is divided into two members, the Lower and Upper Nawata members, with the fossil-bearing rocks dating ~ 7-5 Ma. The Nachukui Formation comprises a Plio-Pleistocene sequence, with the Pliocene units comprising the Apak, Muruongori, and Kaiyumung Members, and the Pleistocene divided into the Kalochoro and Kaitio Members. Most of the Lothagam faunal assemblages have been recovered from the late Miocene of the Nawata Formation, which includes a few tooth specimens that likely represent early hominins. Hominins are definitely known from the Lothagam sequence by the Apak Member (the australopith mandible KNM-LT 329 (Leakey & Harris, 2003).

The Apak Member (Pliocene dated 4.2 Mya), represents an interesting time of faunal change (Fig 3.4). Old late Miocene animals including primitive elephant, were being replaced by more advanced, more hypsodont elephants. It is also a time of climate and environmental change. Wooded savannah and savannah woodland was starting to spread in East Africa (Sanders, 2020).

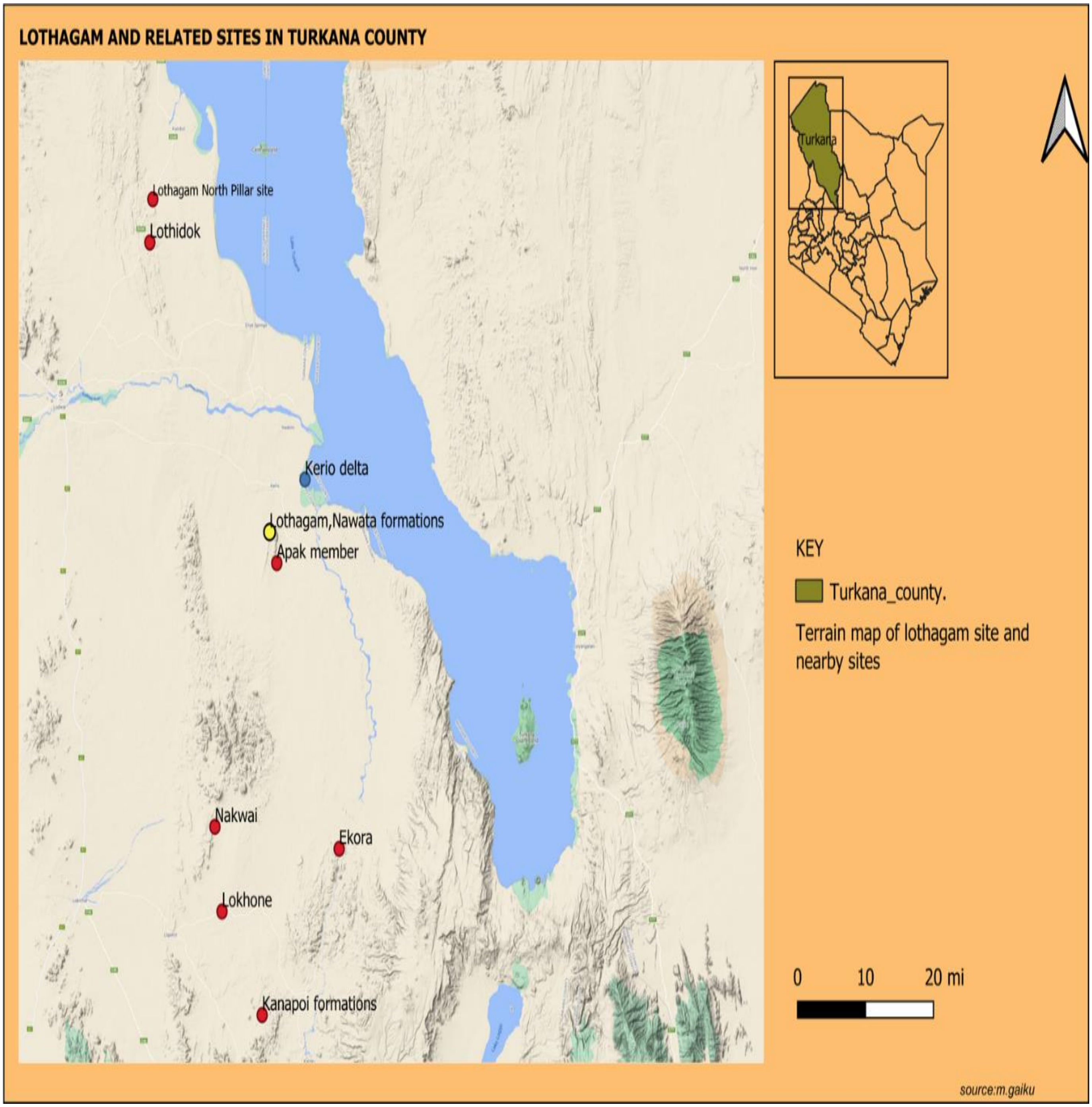

Figure 3.1: Lothagam and related sites in Turkana County

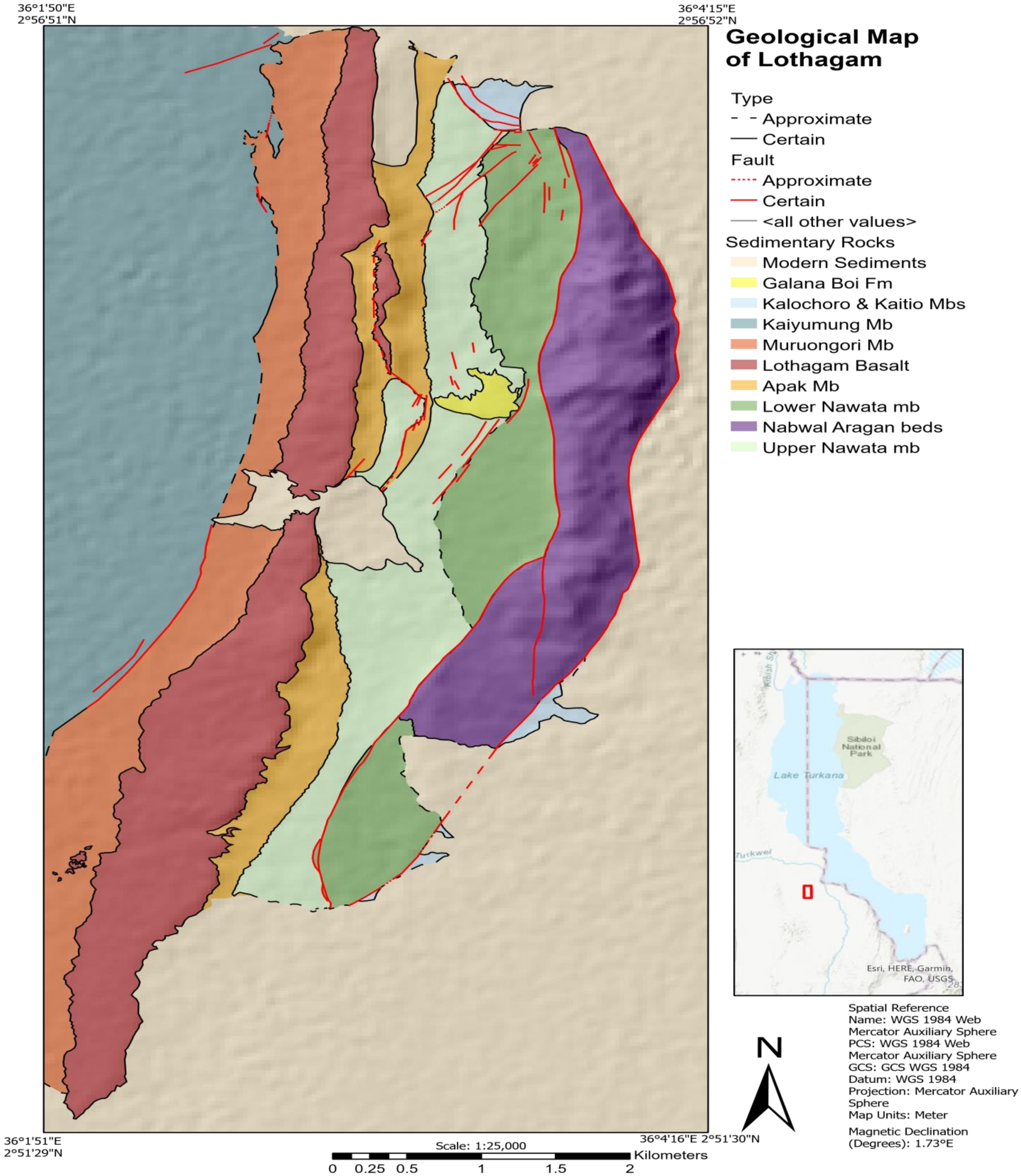

Figure 3. 2: Geological map of Lothagam

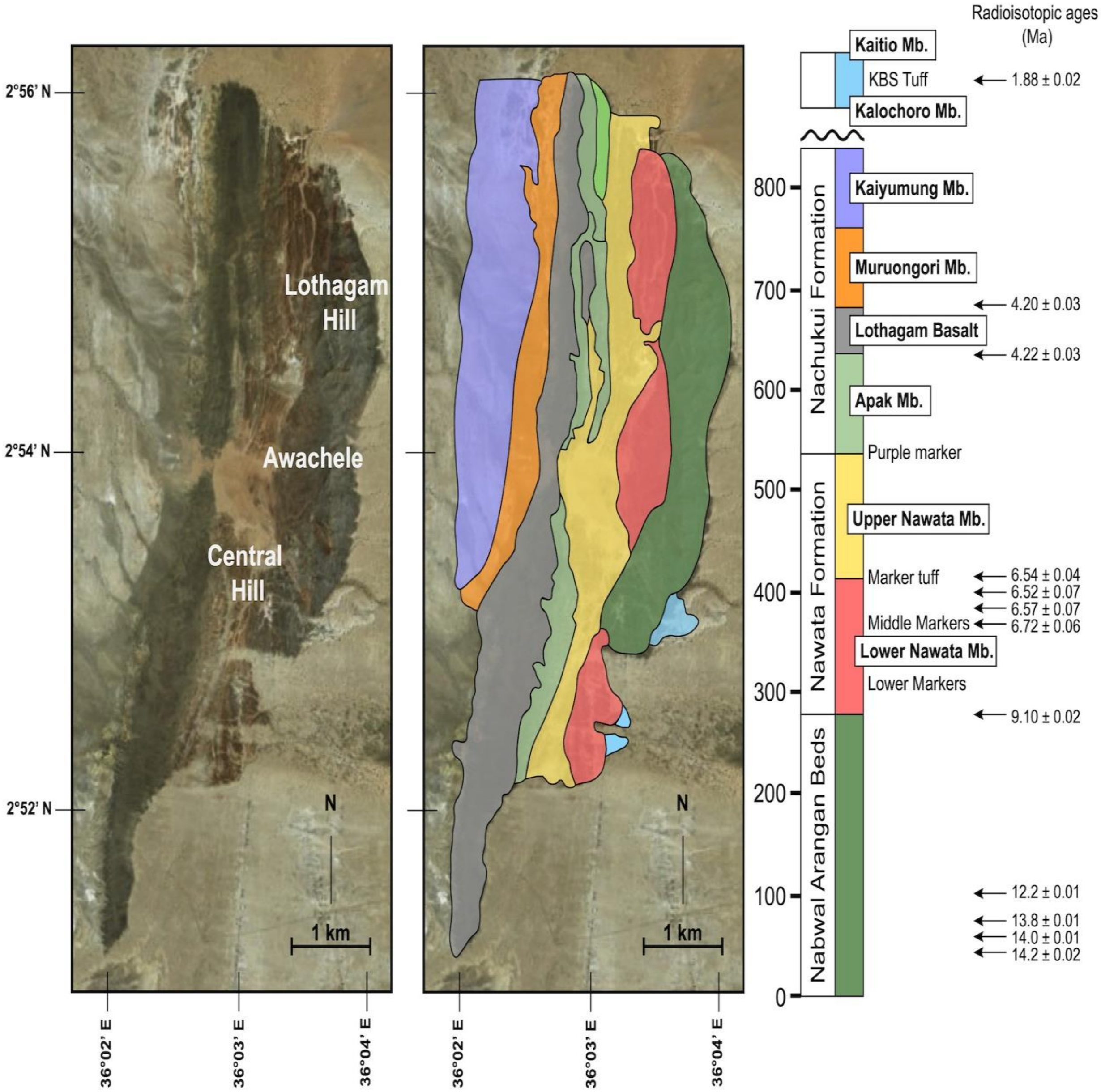

Figure 3. 3: Detailed Geological map of Lothagam

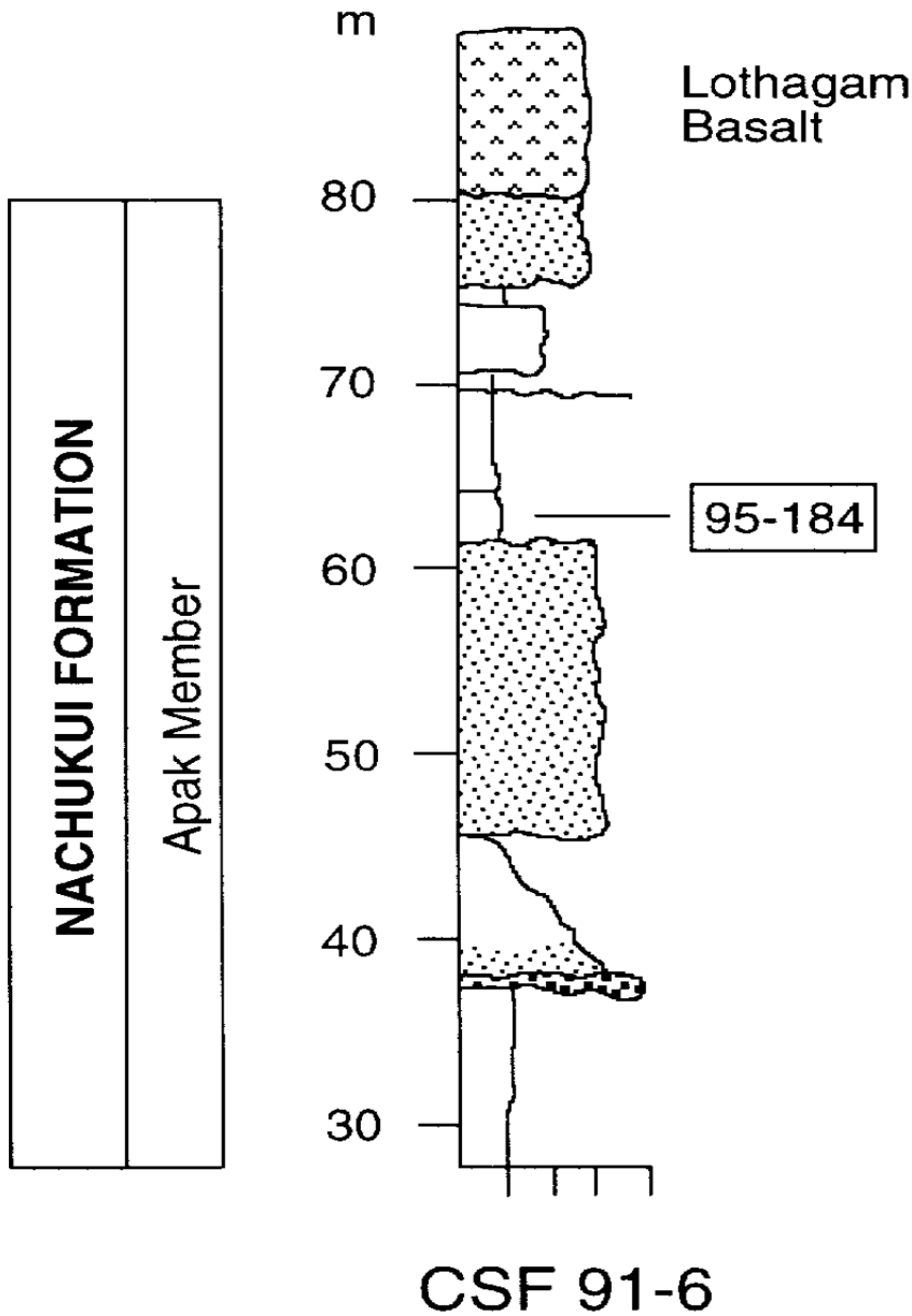

Figure 3. 4: Nachukui formation stratigraphy

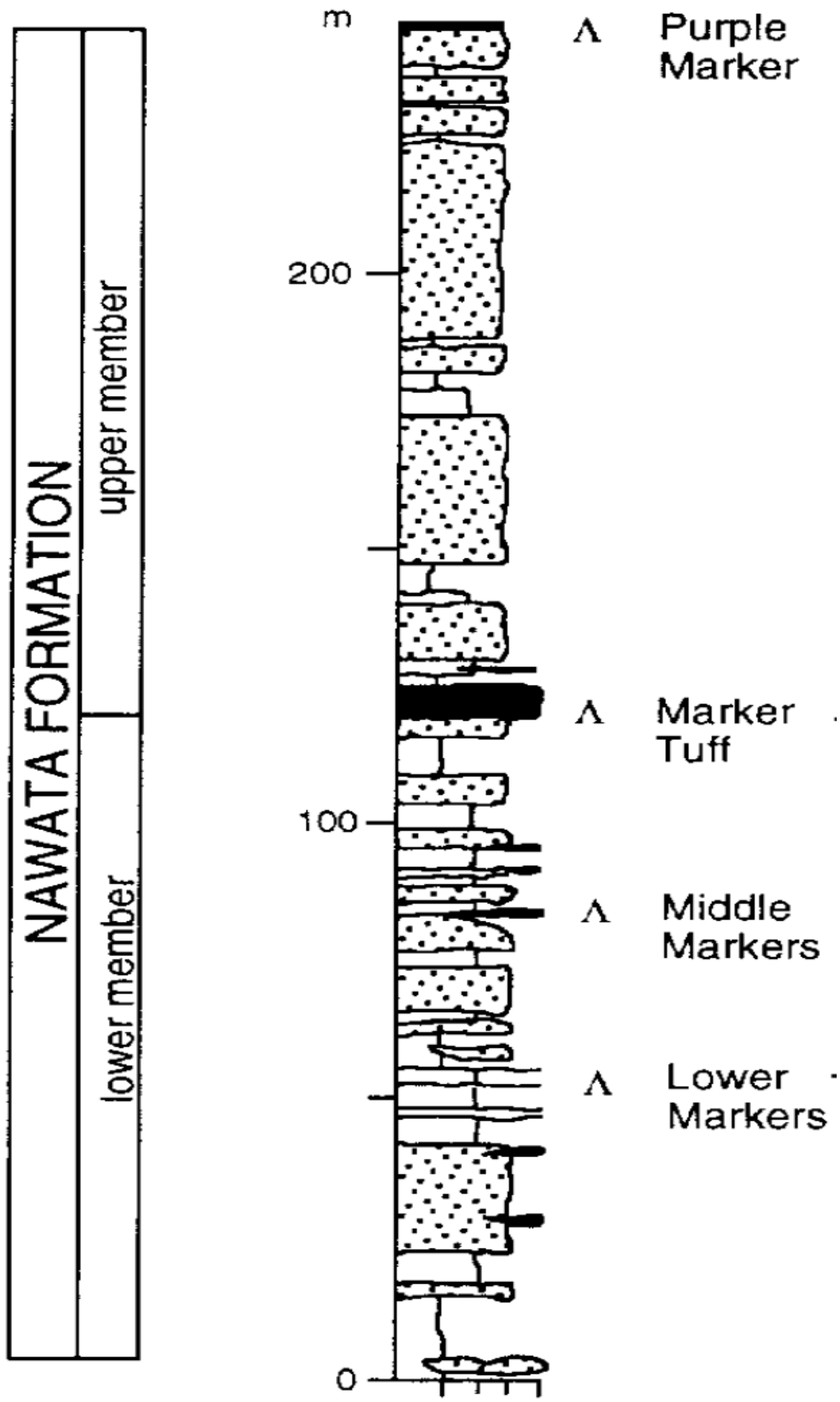

Figure 3. 5: Nawata formation stratigraphy

3.4 Location of specimens

The materials under study and those which have not been studied were safely stored in the Paleontology Lab at Nairobi National Museums of Kenya.

3.5 Materials

A sample size of 12 earlier studied proboscidean specimens and 14 unstudied proboscidean specimens were used (as shown in Table 2.1 and 3.1). Measurements were taken using digital Vanier calipers and a tape measure; a camera was also helpful in taking images of the molar teeth. Additionally, a photo scale/focus guide was also used to indicate the exact interval for each photograph considered.

3.6 Morphometric procedure/sampling procedure

The measurement of different animal species' dental characters is of equal importance to science as collecting data from the field. Different proboscidean teeth differ in size based on how primitive or derived they are. Measuring the length of the proboscidean molar teeth, helps us identify different species. There are various methods of getting data from animal teeth, as has been suggested by (Cooke, 1947 and Sanders, 2020) especially when measuring elephant teeth (Maglio, 1973). Morphometric procedures used to distinguish elephant species include estimation of the degree of enamel folding, enamel thickness, hypsodont index, and expression of accessory conules (Sanders et al., 2021).

Plate number (P): This is sometimes called a lamella or plate. A plate consists of a single enamel fold with dentine or cementum filling on both the anterior conule (ac) or posterior conule (pc) base of the enamel fold, which is joined to similar plates in the front (anterior) and back (posterior). The number of plates was determined by the completeness or incompleteness of the molar tooth. For a complete molar tooth, counting of plates always started at the anterior side as x P1, P2, x. The letter x stands for fused or worn-out plates, which cannot be counted in total (Cooke, 1947; Sanders, 2020; Sanders et al., 2021) also introduced a plus (+) sign, which should always be added to broken or incomplete plates.

Counting for incomplete molar teeth started at the posterior end of the tooth and numbers written in italics as x I, II, III, …… +. If both anterior and posterior ends are broken, the molar tooth is denoted as + I, II, III, …. + (Maglio, 1973) suggested that it was possible to estimate accurately the number of missing plates on incomplete specimens provided the roots are present. The roots are also important because they help to differentiate between upper and lower molar teeth. The upper molar tooth is identifiable as having two roots plus a convex shape on the occlusal surface. The lower molar tooth is identified as having one root and a concave shape on the occlusal surface. (Hay, 1922; Sanders, 2020; Sanders et al., 2021) also suggested that an elephant's complete lower molar tooth can be diagnosed as having a robust anterior root that supports more than three to five plates. So in cases where the root is missing, (Shear & Garutt, 1987) introduced a simple method of estimation of missing plates only if the anterior-most of paired roots and their marker plates are preserved. The crowns of upper teeth tend to be convex and lower teeth concave.

Length (L): The size of the elephant's molar teeth was measured by taking the occlusal surface's total distance from the anterior side to the posterior end of the molar tooth. Scientists such as (Maglio, 973) suggested that measurement taken parallel to the occlusal surface is always smaller than if it was chosen similarly to its crown base. However, measurements were considered accurate when the length is perpendicular to the average lamellar plane since this was the only axis of tooth growth.

Height (H): This was the maximum worn crown height of the tallest plate. Crown height was measured vertically along its length axis, between its apex and lateral base (Beden, 1980).

Lamella frequency (LF): This was the total number of loph(id)s or plates in 100mm (Maglio, 1973) suggested that lamellar frequency can differ depending on tooth type. Due to the convex structure, upper molars recorded lower (LF) than concave-shaped lower molars.

Enamel thickness (ET): The actual enamel thickness varies from plate to plate; some parts of the molar plates were thicker, especially towards the apex and mainly around the sides of the plate and on the median loops. (Aguirre, 1969) suggested that measurements along the crown can be averaged.

Hypsodont index (HI): This measurement was derived by dividing the crown height with the crown width multiplied by 100. Arambourg (1938) was the first researcher to use the relative crown height as an index for the elephant molar hypsodonty. However, (Cooke, 1947) improved this index by multiplying the height/width ratio by 100 to compare different species of elephants. Generally, molars with a hypsodonty index < 75 are brachyodont; between 75 – 99 are mesodont, and greater than or equal to 100 are hypsodonty.

3.7 Imaging

Images and drawings of all proboscidean teeth in the Apak Member of the Nachukui Formation were taken to construct comparisons chronologically.

3.8 Data analysis and presentation procedures

The linear data collected was entered into Microsoft Excel software version 2016 for analysis. The analysis was aimed at getting the percentages of proboscidean species at the Apak Member. The resulting data was compared with older Lothagam proboscideans from the late Miocene and proboscideans assemblages from sites similar to the Apak Member. Data analyzed was presented using graphs, figures, tables, images, and drawings to communicate the findings.

3.9 Ethical considerations

Researchers conducting studies must apply for ethical approval from institutional review boards called research ethics committees. The Research Ethics Committee reviews all research proposals to meet ethical standards and guidelines. NACOSTI, therefore, issued a research permit. The National Museum of Kenya, I was offered an exploration permit to conduct the research. All the handling and safety procedures involved when working with fossils were adhered to.

CHAPTER FOUR

4.0 RESULTS AND DISCUSSIONS

4.1 Introduction

This chapter presents the study results and discussions based on the research findings. The taxonomic classification was based on the first researcher who taxonomically named the species including, the year of classification. This chapter also described all the proboscidean specimen from the Apak Member. The proboscidean species were taxonomically identified using both qualitative and quantitative method of analysis (Appendix 5). Figure 4.1 taxonomically indicate the number of proboscidean at the Apak Member as it was described by (Maglio, 1970, 1973; Tassy, 2003). The results of this study revise taxonomically upward the number of proboscidean specimens at the Apak Member (Fig 4.2).

4.2 Results

The objectives of this study were to describe and taxonomically assign proboscidean dental specimens from the Apak Member assemblage, including specimens not previously studied.

4.2.1 Systematic paleontology

Deinotherium bozasi (Dietrich, 1941)

Referred specimens from Lothagam Apak Member of Nachukui formation, including specimens such as KNM – LT 23677, KNM – LT 23806, and KNM – LT 26345 (Appendix 5 Pg. 68,72 & 74).

Description

All the teeth were extensively worn out and broken but could be described using their dental characters (Appendix 5 Pg. 68, 72 & 74).

Remarks

Deinotheres are a group of archaic early proboscideans that arose in Africa from the Oligocene until the end of the Early Pleistocene. Evidence from the fossil record has been found at 27myr old Chilga in Ethiopia and late Oligocene Losodok, Kenya. They were the only non – elephantimorph taxon species that survived into the Neogene. In the late Miocene-early Pleistocene, these huge animals were found in limited numbers in faunas. Probably, indicating that they were antisocial or did not live close to depositional environments that promoted fossilization (Sanders et al., 2020). Deinotheres are distinguished from elephant species by the downward curvature of the mandibular symphysis and lower tusks and loss of upper tusks. Their downward curved lower molars probably indicated an existence in highly dense environments (Harris, 1978; Sanders, 2011) and suggested that the deinotheres remained browsers until they disappeared in the early Pleistocene.

4.2.2 Systematic paleontology

Elephantimorpha (Tassy and Shoshani, 1997)

Elephantida (Tassy and Shoshani, 1997)

Gomphotheriidae (Hay, 1922)

Anancine (Hay, 1922)

Anancus (Aymard, 1855)

Anancus kenyensis (Macinnes, 1942)

Referred specimens from Lothagam, Apak Member of the Nachukui Fm. KNM – LT 23790, half lower molar, KNM – LT 28567, Lt. dP4, KNM – LT 341, associated portions of Rt. m3, Lt.m3, and Lt. M3 (Appendix 5 pages 86 – 88).

Description

KNM – LT 23790. This specimen is the anterior portion of a left lower molar, M1 or M2. A complete trefoil is present as seen in second plate. Anancoidy is not pronounced, conelets are bulbous, and there is no sign of posttrite accessory conule (Appendix 5 page 88).

KNM – LT 341 (Appendix 5, Pg. 86). These are associated portions of Rt. m3, Lt. m3, and Lt. M3. The third upper molar is not of the same individual. The molar tooth of specimen KNM – LT 341 (A and B) is enormously constructed, with little evidence of accessory conules. Fragment A (341) represents a fragment of the posterior end of the last four plates of an m3. Anancoidy is weak, each side of the lophids has only one conelet, and development of accessory conules is minimal. This presents very primitive crown construction as is found in *Anancus Kenyensis* and not *Anancus ultimus*. Molar fragment B (341) is the posterior half of the crown with the postcingulid and three plates. C (341) is the posterior end of a molar tooth with a plate and postcingulum and is probably a left upper M3 due to the convex shape of the molar tooth.

KNM – LT 28567. Lt. dP4. The tooth is broken at the anterior and lateral sides. The postcingulum consists of two posterior cusps connected to the last plate. Anterior pretrite accessory conules are also present (Appendix 5, Pg. 89).

Remarks

There are several African *Anancus* species: *Anancus kenyensis*, *Anancus petrocchii, Anancus ultiumus, Anancus capensis, and Anancus osiris. Anancus petrocchii* is a late Miocene species only found in Sahabi, Libya. *Anancus petrocchii* is characterized by having pentolophodont intermediate molars, with their third molars having six loph(id)s and very weak anacoidy as described by (Petrocchi, 1943, 1954; Coppens, 1965). Their molar teeth are also said to be enormously constructed. Expression of accessory conules is complex on both pre-posttrite sides.

Anancine gomphotheres have been interpreted as browsers due to their branchyodont and bunolophodont molars (Smart, 1976). However, dental isotopic analysis results indicated that Central and East African anancines were typically mixed feeders with a strong component of C4 grasses in their diets and grazers (Cerling et al., 1999; Harrison & Kinston, 2007).

4.2.3 Systematic paleontology

Elephantidae (Gray, 1821)

Stegotetrabelodon (Petrocchi, 1941)

Stegotetrabelodon orbus (Maglio 1970)

Referred specimens from Lothagam, Apak Member of the Nachukui Formation. KNM – LT 366, upper Rt. M3, KNM – LT 354, Lt. Mand. M2 – 3 & frag., KNM – LT 355, lower Lt. & Rt. M? 3, KNM – LT 359, lower Lt. & Rt. M3 7 upper lt. M3, KNM – LT 26337, molar frags, and KNM – LT 367, right M3 (Table 4.1)

Description

KNM – LT 366, this was the upper Rt M3. The tooth was worn with a course enamel undulation, and anterior and posterior conules were not seen. The posterior end of the tooth was narrow with smooth asymmetrical wear of the enamel. The wear pattern was more pronounced lingually, especially on the first two plates, and on the posterior plates. Wearing was more pronounced labially. The transverse valley was coated with cementum except for the last two plates (Table 4.1). Maglio described this molar tooth (KNM – LT 366) as M2, but Tassy (2003), on the other hand, interpreted the tooth as M3 based on asymmetrical wear. The short size of KNM – LT 366 compared with other M3 species suggested to Tassy that it was from a female elephant if it was an M3. However, it was probably an M2 with a well-developed postcingulum (Appendix 5, Pg. 70).

KNM – LT 355, this was lower Lt & Rt M? 3. This specimen had several molar fragments. Molar tooth A is Rt M3. The tooth was low crowned and broken on the anterior side. The molar tooth had a smooth lamellar folding. Plate 2 had a less pronounced anterior accessory conule than plate 1, with lots of cementum. Both molars A & B are Lt & Rt m3 because of the concave shape usually associated with the lower molar tooth. Molar B = is Lt M3. The tooth was broken on the anterior side. The posterior conule was not well pronounced, the enamel was too thick, and the tooth had less cementum (Appendix 5, Pg. 67).

KNM – LT 354 (type specimen), r.M2-3; l. dentary with m2-3 and i2 (lower tusk). r. M2 = +5x, r. M3 = x6x, l. m2 = +5x, l. m3 = 7x. The symphysis measured 390 mm from the presymphysis to the broken anterior while dentary measured 570 mm from the posterior end to the broken symphysis. The symphysis was also strongly angled on the dentary; the angle of approach of the tusk makes it impossible that its root could have continued into the dentary canal. There was no actual observable connection between the symphysis and the tusk piece as well as the dentary. There are two mental foramina both under the absorbing alveolus for m1. The root of ramus was even in plate 3 of m3. The lower tusks were eccentrically ovoid in cross-section with a trace of a slight lateral sulcus, and there was no apparent enamel band on the tusk.

The m2 had signs of accessory conules behind each plate, strong postcingulid, traces of cementum coating in the valley floors, and plates were broadest basally and posteriorly. The m3 cementum was thick, covering plate walls up to apices but not filling valleys. The plates were primarily composed of four conelets, accessory conules and posterior conule on plates 1-2. The plates were high centrally, and there was no distinct median sulcus. Additionally, the postcingulum was distinct, and formed of two strong pillars. The M2 had posterior accessory conules in plates 1-4. The transverse valleys were V-shaped to sub-U-shaped, and plates seemed to be pyramidal in lateral view. M3 with posterior accessory conules in plates 1-2, formed five conelets. The conelets were massive, especially basally, V-shaped transverse valleys, and there was no median sulcus (Appendix 5, Pg. 63 – 66).

KNM – LT 26337, these were molar frags. The molar tooth was broken and had traces of cementum at the posterior end of the molar tooth (Appendix 5, Pg. 83).

KNM – LT 367. Right M3. The tooth was heavily worn, and it had a coarse undulation of the lamella. There was the presence of posterior accessory conules associated with plates 3 and 4. The molar tooth also had 4-5 conelets per plate, a trace of cementum in transverse valleys. The postcingulum was simple, formed of one or two conelets, plates were pyramidal in shape and massive, and very thick enamel (Appendix 5, Pg. 71).

Remarks

Stegotetrabelodonts, as described by Sanders et al. (2010) and Maglio (1973), was identified by retaining primitive features such as P3 – 4 / p3 – 4 and lower tusks. Other essential features included few plates or loph (id)s, very brachyodont or low crowned molars, pyramidal plate shape, very thick enamel, weak/low covering of cementum, and low lamellar frequency (Maglio, 1973; Sanders et al., 2010).

4.2.4 Systematic paleontology

Primelephas (Maglio, 1970)

Primelephas korotorensis (Maglio, 1970)

The described specimen from Lothagam, Apak Member of Nachukui formation included specimen KNM – LT 363, which was mandibular symphysis, and partial Rt. M3 (Appendix 5, Pg. 87).

Description

KNM – LT 363, 2 mandible symphysis & partial Rt. M3. The molar tooth was broken anteriorly and had only one plate with an extended posterior conule. Maglio described the specimen as *Primelephas "gomphotheroides"* with a partial right M3 and a mandibular symphysis. Later, Tassy (1986) allocated specimen KNM – LT 363 to *Stegotetrabelodon orbus* based on similarities in dental characters, and he also noted that the mandibular symphysis does not belong to the same species (Appendix 4, table 4.1).

Remarks

Primelephas koroterensis is characterized by low-crowned molars with broad snout plates. This species also has strong grooves that divide the molar plates into prominent columns. The plates appear to be pyramidal when viewed longitudinally and widest at the base. The transverse valley is not filled with cementum and seems open at the base. The species has unfolded thick enamel, and the lamellar frequency is low.

4.2.5 Systematic paleontology

Loxodonta cookei (Sanders 2007)

Referred specimens from Lothagam, Apak Member of Nachukui formation. KNM – LT 26321, worn anterior portion of m3, KNM – LT 23786, Lt. M3, KNM – LT 23794, Rt. M3 fragment (Appendix 5, Pg. 75 & 76).

Descriptions

KNM – LT 23786 (Appendix 5, Pg. 75), which was M3. The specimen had very large/huge conulets, thick enamel. The molar tooth was worn out and broken anteriorly. The tooth had 3 – 4 conulets per plate or more. The tooth had a definite marked midline expansion of the central pillar, suggesting a nascent *loxodont* sinus, probably incorporating anterior and posterior accessory conules into enamel wear to figure in plate II. The enamel was unfolded, and the cementum was invested in transverse valleys. The tooth also appeared to be too primitive to be *Loxodonta exoptata*. Thus, it was probably *Loxodonta cookei*, known from late Miocene to early Pliocene in eastern and southern African sites (Sanders, 2007). The crown tapered posteriorly. Only the posterior fragment of plate IV remains broken anteriorly. The convex shape indicated that it was an upper molar tooth (Table 4.1).

KNM – LT 26321, worn anterior portion of m3. The molar tooth was worn with four plates from the anterior end. The tooth had a course lamella folding with both the anterior (ac) and posterior (pc), touching each other from adjacent plates. The transverse valley was filled with abundant cementum. The concave shape of the occlusal surface indicated a lower molar, and the shape of the plate in the occlusal view was almost rectangular (Appendix 5, Pg. 81).

KNM – LT 23794 (Appendix 5, Pg. 76), was a partial right M3. The incomplete molar tooth consisted of a plate formula of +1/2 5x. All the plates were worn except the two posterior cusps. The molar tooth was filled with cementum visible on the preserved five plates. (Tassy, 2003) identified molar as aff. *Loxodonta exoptata*, prior to *Loxodonta cookei* being recognized as a more primitive species in the *Loxodonta exoptata* lineage (Sanders, 2007). The transverse valley was open and filled with cementum. The plates were parallel-sided. Transverse valleys were correspondingly U-shaped at the base. Additionally, the molar tooth had ropeller-shaped arms and prominent central sinus in each enamel wear figure. This characteristic indicated that, anteriorly and posterior expansions of enamel touched in the midline. There were 5-7 conelets per plate. Enamel was roughly and irregularly undulated in places and coarsely folded medially but smooth laterally.

Remarks

Loxodonta exoptata, as described by (Beden 1987a; Sanders et al., 2010; Sander, 2011), was a Pliocene species best known in the Upper Laetolil Beds Tanzania, at the type site of Laetoli. *Loxodonta exoptata* was distinguished from *Loxodonta adaurora* and *Loxodonta cookei* by its more significant number of molar loph(id)s or plates (about eleven, especially in m3s), with thinner enamel, higher molar crowns (higher hypsodonty), development of loxodont sinuses, prominent postcingulum, and a greater enamel folding at the base of the third molar plate. Compared to *Elephas ekorensis*, *Loxodonta exoptata* appears to have accessory conules that are not cylindrical, especially throughout their height but seem to increase in width towards their bases (Beden, 1987 a; Sanders, 2011). *Loxodonta exoptata* is described by (Sanders, 2011) and Beden, 1987 a) as phylogenetically closely related to modern African elephants that are presumed to belong to the *Loxodonta cookei* lineage of the late Miocene to early Pliocene. Results from carbon isotope dental analysis indicate that *Loxodonta exoptata* was primarily a mixed–feeder with some C_4 grasses in their diets (Cerling et al., 1999; Kingston, 2011. It also seems likely, given the primitive condition of the molars tentatively assigned to *Loxodonta exoptata* by (Tassy, 2003). The thick enamel, for example indicate that the Apak Mb. sample belongs instead to *Loxodonta cookei*.

4.2.6 Systematic paleontology

Elephantidae (Gray, 1821)

Elephantinae (Gray,1821)

Loxodonta (Cuvier, 1825)

Loxodonta adaurora (Maglio, 1970)

Described materials from Lothagam, Apak Member of the Nachukui Formation. KNM – LT 26320, Left dentary with dp4 and erupting m1, KNM – LT 26340, tooth frags, KNM – LT 353, broken skull of m3, and KNM – LT 26320, was a Left dentary with dp4 and erupting m1 (table 4.1).

Description

KNM – LT 26320 (Appendix 5, Pg. 80), this was a left dentary with dp4 and erupting m1- *cf. Loxodonta adaurora*. Looking at the dental morphological characteristics, the molar tooth was a left dentary with dp4 and emerging m1. The plate number was modest, with seven plates in each tooth. This was typical in number for *Loxodonta adaurora* and too few for *Elephas ekorensis* (Sanders, 2020). The anterior and posterior accessories associated with each plate were typical of *Loxodonta adaurora* and differed from other non–*loxodont* elephant molars. The plate shape of the m1 was most expansive at the base and curved towards the apex, also typical for *Loxodonta adaurora*. The small folding of enamel in the enamel loops was characteristic of deciduous premolars, even in some early elephant species. Cementum covered the plates of m1 but did not infill the transverse valley between them. The m1 plates were formed of between three and four conelets.

KNM – LT 26340, this was tooth frag. Molar A: The tooth was worn and broken at the anterior side, plate 1 had both anterior and posterior conules, the tooth had no evidence of cementum, and it was a *Loxodonta* species because of the sinuses. Molar B was badly worn out and had no proof of cementum. Molar fragment C is broken and part of a molar's posterior end (Appendix 5, Pg. 84).

KNM – LT 353 (table 4.1), This was broken cranium with M3. According to Maglio (1973), the tooth plate formula was 10x. Maglio, (1973) also indicated other measurements as follows; L = 268.9, W = 107.2(3), LF = 3.9, H = 106.7, HI = 91, ET = 3.7 – 4.8, and the tooth occlusal surface was heavily worn. The tooth had fine enamel folding and abundant cementum. However, despite the tooth being broken, it had a convex occlusal surface, indicating an upper molar. The specimen was missing in the NMK collections (Appendix 5, Pg. 63).

Remarks

Loxodonta adaurora is more derived than its predecessor archaic species of the late Miocene and is found in many eastern African Pliocene sites, particularly around the Lake Turkana basin (Sanders, 2020; Sanders et al., 2021). The species has been divided into successive subspecies by Beden (1983) and Maglio (1973); the subspecies include *Loxodonta adaurora adaurora* and *Loxodonta adaurora kararae.* The subspecies have been documented in various early Pliocene to early Pleistocene sites of eastern Africa. These sites are comprised of Kanapoi, Kenya (Sanders, 2020), Tugen Hills, Kenya (Maglio, 1973), Mursi Formation, and Member B, Shungura Formation, Omo, Ethiopia (Beden, 1987b), West Turkana, Kenya at lower Lomekwi Mbs. and Kataboi (Harris et al., 1988), Allia Bay, Kenya at Koobi Fora Formation (Biden, 1983), Ekora, Kenya (Maglio, 1970, 1973), Apak Member of Nachukui Formation, Lothagam Kenya (Maglio, 1970, 1973), Ileret, Kenya, Koobi Fora Formation, Kenya, Middle Awash, Ethiopia, possibly at Denen Dora and Sidi Hakoma Members (Sanders, 2020; White et al., 1984) and western Rift Uganda at Nkondo Formation (Sanders, 1990).

The species (*Loxodonta adaurora*) was distinguished by having molars with a modest number of well-spaced plates. Other distinguishing characteristics of *Loxodonta adaurora* include low crowned molar teeth, thick, unfolded, or coarsely folded enamel, laterally curved plate profiles, presences of posterior, strong central conelets, and salient posterior-anterior conules (Sanders, 2020). *Loxodonta adaurora* had fewer plates, thicker enamel, and lower crown heights (usually hypsodonty indices < 100 than *Loxodonta exoptata* and *Elephas recki* (Sanders et al., 2010).

4.2.7 Systematic paleontology

Elephas ekoresis (Maglio, 1970)

Referred specimens from Lothagam Apak Member of Nachukui formation, KNM – LT 23795, 1.M1, KNM – LT 23581, broken M1 (Table 4.1).

Description

KNM – LT 26581, this was a broken M1. The tooth was extensively worn out, was smaller than m3(s), and had fine enamel folding (Appendix 5, Pg. 85).

KNM – LT 23795B (Appendix 5, Pg. 77), partial left M1 fragment. The tooth had a convex occlusal surface, showing an upper molar. A narrow precingulum precedes the most worn enamel loop. Plate 1 had a tiny ac1 and pc1; plates 2-3 had a more prominent posterior conule (pc2-pc3). The tooth had coarse folding or undulation of enamel loops. Enamel thickness was modest. Tassy (2003) identified this specimen as *Elephas* cf. *ekorensis.* Weak or absent expression of anterior accessory conules and posterior accessory conules behind each plate signaled that this was likely not a molar of *Loxodont.* The tooth does not seem archaic enough in morphology to be a *Stegotetrabelodont* or from *Primelephas.* Cementum was present in the transverse valleys between the plates (Table 4.1).

Remarks

According to the description by Maglio (1970), *Elephas ekorensis* is distinguished from *Loxondonta adaurora* by having a more significant number of plates (11-12, especially in M3s), narrowing of the posterior crown, and molars slightly hypsodont (Sanders, 2020). *Elephas ekorensis* is poorly represented in most eastern African Pliocene sites. In Kenya, the species has been recorded from Ekora; other places include Kaiso Formation, Uganda (Maglio, 1973; Ricca, 1977). According to Tassy (1986), the species was represented in the Apak Member by specimen KNM – LT 23795 - partial Rt. M1 and KNM – LT 26320 – Hemi – mandible with dP, and m1. This study indicated that *Elephas ekorensis* is represented in the Apak Member by specimens KNM LT 23795, KNM LT 26581, and KNM LT 23799. These specimens presented more derived traits and were closer to the Pliocene elephantine of about 4.2 million years ago.

4.2.8 Systematic paleontology

Elephantidae *gen.* and *sp. Incertae sedis B*

Referred specimen from Lothagam, Apak Member of Nachukui Formation. KNM – LT 26323, posterior portion upper M3 and tooth fragments.

Description

KNM – LT 26323 posterior portion upper M3 and tooth fragments. In a study of dental isotopes, the specimen was listed as *Primelephas gomphotheroid*es. The concave shape indicated a lower right molar. The tooth was an m3 because of the tapered posterior end. Plate 1 of the molar tooth showed the presence of posterior conule and no evidence of accessory conules. The tooth was broken at the anterior side, had less cementum, and had a thinner enamel thickness (ET) of 3, Lamella frequency (LF) = 4, P = 4, L = 131.07, and width (W) of 75 at plate 2 (Appendix 5, Pg. 82).

Remarks

The specimen KNM – LT 26323 belonged to Nawata Formation and not Nachukui Formation, as it was earlier indicated. The dental morphological characteristics were similar to those represented by *Stegotetrabelodon orbus.* The characteristics included very low crowned molar teeth, pyramidal plate shape, thick enamel, low lamellar frequency, and weak cementum covering (Maglio, 1973; Sanders et al., 2010).

4.3 Discussion

There are several new findings derived from this study. Descriptions done by (Maglio, 1970, 1973 and Tassy, 2003) to specimen KNM – LT 354 (type) were incomplete. That is, some elements of the specimens were left out**.** The specimen is significant because it suggests that the plate formula or M2/m2 is pentalophodont (five plates) and that M3/m3 has plates/loph(id)s of 6 or 7. The tooth enamel is very thick**.** This differs from the condition in *Stegotetrabelodon syrticus* and *Stegotetrabelodon emiratus*. The third molars only have good accessory conules behind plates 1 and 2 but, not throughout the entire crown.

Specimen KNM – LT 26320, based on its occlusal morphological characteristics, is a left dentary with dp4 and erupting m1. The tooth was earlier identified as *Elephas c.f ekorensis* by Tassy (2003), Maglio and Rica (1977); and Maglio (1970, 1973), but plate number and morphology are consistent with *Loxodonta adaurora (*Sanders et al., 2020; Sanders, 2011; Biden, 1987a).

The specimen KNM – LT 26340 is *Loxodonta adaurora* but not *Elephas ekorensis* as Maglio described earlier in 1970, 1973, and Tassy, 2003. These conclusions are based on studies done by Sanders et al., 2010; Sanders et al., 2020; Cerling et al., 1999). Specimen KNM – LT 23786 is too primitive to be *Loxodonta exoptata* based on studies done by (Sanders, 2011, 2020; Biden, 1987a) probably; this specimen is *Loxodonta cookei*.

Specimen KNM – LT 23795 B was earlier described by Tassy, 2003 as *Elephas cf. ekorensis*. Maglio, 1973, described the specimen as partial right upper third molar, and the species name as *Loxodonta sp.* aff *Loxodonta exoptata.* This study results indicate that weak or absence of expression of anterior accessory conules and presence of posterior accessory conules behind each plate signal that this specimen is likely not a molar of *Loxodonta;* and it does not seem archaic in morphology to be a *Stegotetrabelodon*t or *Primelephas* (Sanders, 2020, 2021; Cerling, 2003).

The specimen KNM-LT 23794 was identified by (Tassy, 2003) as aff. *Loxodonta exoptata*, prior to recognizing *Loxodonta cookei* as a species (Sanders, 2007, 2008, 2020,2021). The third molar, described as KNM – LT 341**C,** did not tally with characteristics exhibited by *Anancus* as described by (Maglio, 1970, 1973; Tassy, 2003). However, the specimen has similar characteristics to elephant molars based on the presence of accessory conules on a molar tooth. (Mackaye, 1942) in Chad, was responsible for changing *Primelephas* g*omphotheroides* into *Primelephas koroterensis*, and this is to recognize a mistake made by (Maglio,1973).

Specimen KNM – LT 353, (Maglio, 1973) erroneously listed the specimen in his publication as KNM – LT 383. Characters identified for this specimen by (Maglio, 1973) as having loxodont sinuses in the midline of enamel loops could suggest that this specimen is not *Loxodonta adaurora*. Specimen KNM – LT 353 was also not published by (Tassy, 2003). (Maglio, 1973) on the other hand, described the specimen as a skull with left M2-3, right M3, and left tusk from Lothagam 3. However, information from the comment slip indicates that the specimen KNM – LT 353 was loaned to Harvard University and extensively damaged on its return journey. The specimen is missing from NMK. Therefore, the upper third molar tooth is presently the only part of the skull available for study. Specimen KNM – LT 23785, described by (Maglio, 1973; Tassy, 2003) as Incertae sedis A, is not from the Apak Member of the Nachukui Formation but the Nawata Formation.

CHAPTER FIVE

5.0 CONCLUSION AND RECOMMENDATIONS

Introduction

This chapter intended to present the conclusions and recommendations of the research study based on the research findings.

5.1 Conclusions

Field work conducted at Lothagam by Bryan Patterson and team in 1963 to 1968, Meave and Leakey, and Koobi Fora Research project (KTRP) in 1980, and in 1989 – 1993 by National museums of Kenya expedition has proved that the elephantoid diversity especially in the Apak Member is greater than it was earlier anticipated. The presence of *Anancus*, *Primelephas*, *Stegotetrabelodon*, *Deinotherium*, *Loxodonta cookei*, *Elephas* aff. *ekorensis* and more *Loxodonta adaurora* was confirmed.

Our results meaningfully revise and increase the taxonomic composition of proboscideans in the Apak Member sample, revealing a complex relay of primitive to more derived elephants during the early Pliocene that documents the adaptive response to increased competition among mammals for grazing resources (figure 4.2). It is also worth noting that tetra and pentalophodont gomphotheres persisted in East Africa up to mid – Pliocene and not late Miocene. Lothagam materials especially the Apak Member, also proved existence of *Stegotetrabelodonts* unlike earlier reports by previous researchers, which indicated that they were absent. Additionally, Kenyan *Stegotetrabelodonts* are more derived compared to the Libyan and Arabian *Stegotetrabelodon* species.

Those results also indicated the possibility of the presence of *Loxodonta cookei* from the late Miocene to early Pliocene of eastern and southern Africa. The results of this study also show that there was a coexistence of *Stegotetrabelodonts*, *Primelephas*, and possibly several species of *Loxodonta*, *Anancus*, and *Deinotherium* which all belong to the Apak Member. These results suggest an ancient ecosystem that is very unlike many modern ecosystems in Africa, based on its ability to simultaneously support so many immense – sized proboscideans.

5.2 Recommendations

The most important thing that remains to be done with the study of the Apak Member proboscideans; This study suggest that additional collections should be made with a much greater dedication to precisely locate the fossils in the stratigraphy of the Member (to confirm the date). Many or most of the previous fossils collected in the Apak Member do not have precise stratigraphic_information and this is important to confirm if these proboscideans truly lived side by side.

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APPENDICES

APPENDIX 1: WORK SCHEDULE

Table 1. 1: Work schedule

Dates	Activity
January 10	Thesis topic and paragraph description
January 15	First outline (2pages)
February 1	Second outline (5pages)
February 28	Begin first draft (10 text pages)
March 10	Discuss the first draft with supervisors
March 15	Write a second draft (15 text pages max and citations)
March 25	Discuss the second draft with supervisors
March 30	Begin final draft (15 text pages max and citation)
April 5	Discuss final draft with supervisor
November 4th, 2020	Thesis proposal defense (Turkana University College)
November 7 – Dec 2020	Data collection (Nairobi National Museums of Kenya, Paleontology Lab)
January 5, 2021	Results (National Museums of Kenya, Paleontology Lab)
January 30 – July 29, 2021	Dissertation writing
July 30, 2021	Present first draft thesis soft copy to supervisors
August 30, 2021	Present second draft thesis copy to supervisors
September 30, 2021	Present final soft and hard copies of the thesis to supervisors.
The first week of October 2021	Oral thesis defense
October 15, 2021	Submission of final original bound thesis copy

APPENDIX 2: PROBOSCIDEAN SPECIMENS

Table 2.1: Referred specimens from Lothagam.

Taxonomic classification	**Referred specimens from Lothagam, Apak Member of the Nachukui Formation.**
Elephantidae (Gray, 1821) Stegotetrabelodon (Petrocchi, 1941) *Stegotetrabelodon orbus* (Maglio 1970)	KNM – LT 366, upper Rt. M3, KNM – LT 354, Lt. Mand. M2 – 3 & fragments., KNM – LT 355, lower Lt. & Rt. M? 3, KNM – LT 359, lower Lt. & Rt. M3 7 upper lt. M3, KNM – LT 26337, molar frags
Primelephas (Maglio, 1970) *Primelephas korotorensis* (Maglio, 1970)	KNM – LT 363, 2 mand symphysis & partial Rt. M3.
Elephantidae gen, and sp. *incertae sedis* A	KNM – LT 23785, a portion of Rt. M3.
Elephantidae gen. and sp. *incertae sedis* B	KNM – LT 26323, posterior portion upper M3 + tooth frags.
Elephas ekorensis (Maglio, 1970)	KNM – LT 26320, Lt. mand. dm3 erupting m1, KNM – LT 23795, 19 skull frags. + M_ fragments plus tusk fragments, KNM – LT 23581, Broken m1.
Loxodonta cookie (Dietrich, 1941)	KNM – LT 26321, worn anterior portion m3, KNM – LT 23786, Lt. M3, KNM – LT 23794, Rt. M3 fragments.
Loxodonta adaurora (Maglio, 1970)	KNM – LT 26340, tooth fragments, KNM – LT 353, broken skull of m3.

Elephantimorpha (Tassy and Shoshani, 1997) Elephantida (Tassy and Shoshani, 1997) Anancine (Hay, 1922) Anancus (Aymard, 1855) *Anancus kenyensis* Macinnes, 1942	Referred specimens from Lothagam, Apak member of the Nachukui Fm. KNM – LT 23790, half lower molar, KNM – LT 28567, Lt. dP4, KNM – LT 341, associated portions of Rt. m3, Lt.m3, & Lt. M3.
Loxodonta aff. *exoptata* (Dietrich, 1941)	KNM – LT 26321, worn anterior portion m3
*Deinotherium bozasi (*Dietrich, 1941)	Referred specimens from Lothagam, Apak member of the Nachukui Fm. KNM – LT 23877, Rt. dp4 fragment, KNM – LT 23806, molar fragments, KNM – LT 26345, molar fragments.

APPENDIX 3: PROBOSCIDEAN SPECIMENS

Table 3.1: Previously studied specimens

Accession Number	**Previously assigned Taxon**	**Part**
KNM – LT 26323	Incertae sedis B (from isotope study, indicated to be *Primelephas gomphotheroides*)	Posterior portion upper M3 + tooth fragment.
KNM - LT 26320	*Elephas ekorensis* (comment slip *Loxodonta adaurora*)	Lt. mand. dm3, erupting M1
KNM - LT 341	*Anancus kenyensis*	An associated portion of right m3left m3 and left M3
KNM – LT 23790	*Anancus kenyensis*	The anterior portion of M2-3
KNM – LT 354 (Holotype)	*Stegotetrabelodon orbus* [Apak Mb. OR Upper Nawata Fm.]	Lt. mand. m2 -3 & fragments
KNM - LT 363	*Primelecphas gomphotheroides*	2 mand. symphysis & partial right M3
KNM – LT 365	*Stegotetrabelodon orbus* [horizon unknown]	Right M3, right dP3
KNM – LT 366	*Stegotetrabelodon orbus* [horizon unknown]	Right M3 [probably l. M2]
KNM – LT 367	*Stegotetrabelodon orbus* [horizon unknown]	Right M3
KNM – LT 23795	*Elephas* cf. *ekorensis*	Partial right M3 (Maglio denoted it as M1)
KNM – LT 23786	*Loxodonta*? aff *exoptata*	Posterior left m3
KNM – LT 26321	*Loxodonta exoptata* [originally *Primelephas gomphotheroides*] [middle Apak Mb.]	Worn anterior part right m3

Table 3.2 Unstudied specimens

Accession number	**Taxon**	**Part**
KNM – LT 23794	*Loxontoda*? aff *exoptata*	Right m3 fragment
	Stegotetrabelodon orbus [?Apak OR Upper Nawata]	Lower left & right m3
KNM – LT 26337	? *Stegotetrabelodon*	Molar fragment
KNM – LT 353	*Loxodonta adaurora*	Broken skull (m3)
KNM – LT 26581	*Elephas ekorensis*	Broken m1
KNM – LT 26340	*Elephas ekorensis*	Tooth fragments
KNM – LT 379	*Primelephas gomphotheroides* now *Primelephas koroterensis*	2 molar frags + 1 tusk frag
KNM – LT 28567	Elephantidae	Molar tooth
KNM – LT 26345	*Deinotherium bosazi*	Molar fragment
KNM – LT 23677	*Deinotherium bosazi*	Molar fragment
KNM – LT 23799	*Elephas ekorensis*	3m frags+ tusks frags
KNM – LT 23806	*Deinotherium bosazi*	Molar fragment
KNM – LT 23797	*Loxodonta adaurora*	Molar fragment + 19 bits
KNM – LT 23799	*Elephas Ekorensis*	Molar fragment

APPENDIX 4: MEASUREMENTS

Table 4.1 Measurements (in mm) for dentition of all proboscideans from the Apak Member at Lothagam. Abbreviations: dp/dp, upper/lower deciduous premolar; E, enamel thickness: H, height; HI, hypsodonty index (H multiplied by 100/W); I, left; L, length; M/m, upper/lower molar (for example M1 is first upper molar); P/p, upper/lower premolar (for example P3 is upper third premolar); r, right: W, width: P, number of plates (example 1,2,3, 4... plate number counted from anterior of the crown; I, II, III, plate number counted from posterior of the crown); LF, lamella frequency; x, anterior or posterior cingulum (id); +, indicate missing morphology; numbers in parentheses indicate the plat number at which the measurements was taken;? Means tentative identification to a taxon.

	P	L	W	LF	H	ET	HI
KNM – LT 354 r. M2	+5x	+160.5	92.6 (4)	3.25	worn	5.5 – 7.0	--
KNM – LT 354 r. M3	x6x	238.2	104.3	--	74.0	unworn	71
KNM – LT 354 l. m2	+5x	+166.6	90.0 (5)	3.4	worn	6.0	--
KNM – LT 354 l. m3	x7x	276.7	92.5	3.0	88.0 (3)	--	--
KNM – LT 355 A r. m3	x1/2 2x	x101.1	84.9 (II)	--	worn	5.5	--
KNM – LT 355 B l. m3	+2x	+ 91.0	81.0 (II)	--	worn	5.5	--
KNM – LT 365 r. dp3	+5+	59.7	35.4 (4)	--	worn	2.4	--
KNM – LT 26337 A Molar fragment	+2+	56,5	--	--	--	--	--
KNM – LT 26337 B Molar fragment	+2+	43.5	--	--	--	--	--
KNM – LT 26337 C Molar fragment	+2+	38.8	--	--	--	--	--
KNM – LT 366 l. M2	x5x	173.1	83 (3)	4.0	worn	5.5	--
KNM – LT 367	x6x	231.7	101.3 (3)	3.0	worn	6.0	--

r. M3							
KNM – LT 26340 A	+2x	34.3	34.5(2)	--	--	2.0	--
Tooth fragment							
KNM – LT 26340 B	+2x	27.6	43.3 (2)	--	--	--	--
Tooth fragment							
KNM – LT 26340 C	+2x	22.7	45.0 (2)	--	--	--	--
Tooth fragment							
KNM – LT 353	+9x	272.5	91.3 (II)	6 .0	worn	--	--
Partial skull (m3)							
KNM – LT 26326 A	x7x	121.7	54.4 (5)	6 .0	worn	2.3	--
Left mandible dP4 erupting							
KNM – LT 26326 B	x7x	122.6	55.6	6.0	worn	2.3	--
Left mandible dP4 erupting							
KNM – LT 26320	x7x	121.7	59.0 (6)	--	worn	--	--
dp4							
m1	x7x	--	--	5.5	--	--	--
KNM – LT 26321	+3x	+ 71 .2	72.2 (4)	--	worn	3.7	--
l? m2							
KNM – LT 23786	+4x	+150.4	109.7(III)	--	worn	5.7 – 6.1	--
r. m3 or l. M3							
KNM – LT 23794	+1/2 5x	+154.0	93.7 (V)	4.5	worn	4.3 – 4.7	--
r. m3							
KNM – LT 23795	+3x	+75.3	67.6 (3)	--	worn	3.1	--
l. M1							
KNM – LT 26581	+7x	+109.72	47.9 (3)	4.0	worn	--	--
Broken M1							
KNM – LT 23799	+4x	+61.8	51.2 (3)	6.0	worn	--	--
Molar fragment							
KNM – LT 26345	--	--	--	--	--	--	--

Tooth fragments							
KNM – LT 23677	+3+	--	--	--	--	--	--
Rt. dP4 fragment							
KNM – LT 23806	--	--	--	--	--	--	--
Molar fragments							
KNM – LT 379	+1+	--	--	--	+40.0	5.4	--
Molar plate							
KNM – LT 363	+3x	+81.0	84.4 (I)	--	55.0	--	--
Molar plate r.? M2							
KNM – LT 341 A	+1x	+58.9	50.0	4.0	worn	4.0	--
r.m3							
KNM – LT 341 B	+3x	+108.2	62.8 (II)	4.0	worn	4.0	--
I.m3							
KNM – LT 341 C	+4x	+106.0	69.3 (I)	4.0	worn	4.0	--
I.M3							
KNM – LT 23790	+2x	+63.4	60.2 (II)	4.0	worn	--	--
I.M1 or M2							
KNM – LT 26323	+4x	+129.0	+90.3 (III)	--	worn	3.0 - 3.4	--
?Upper molar							

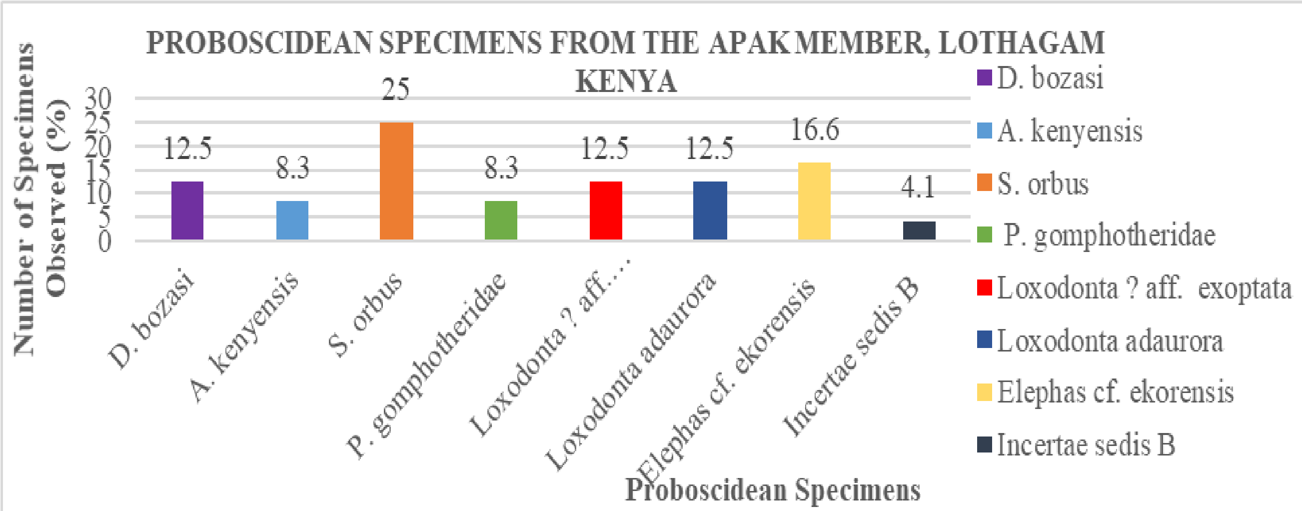

Figure 4.1: Showing proboscidean specimens in percentages % as described by (Maglio, 1970,1973; Maglio and Ricca, 1977; Tassy, 2003).

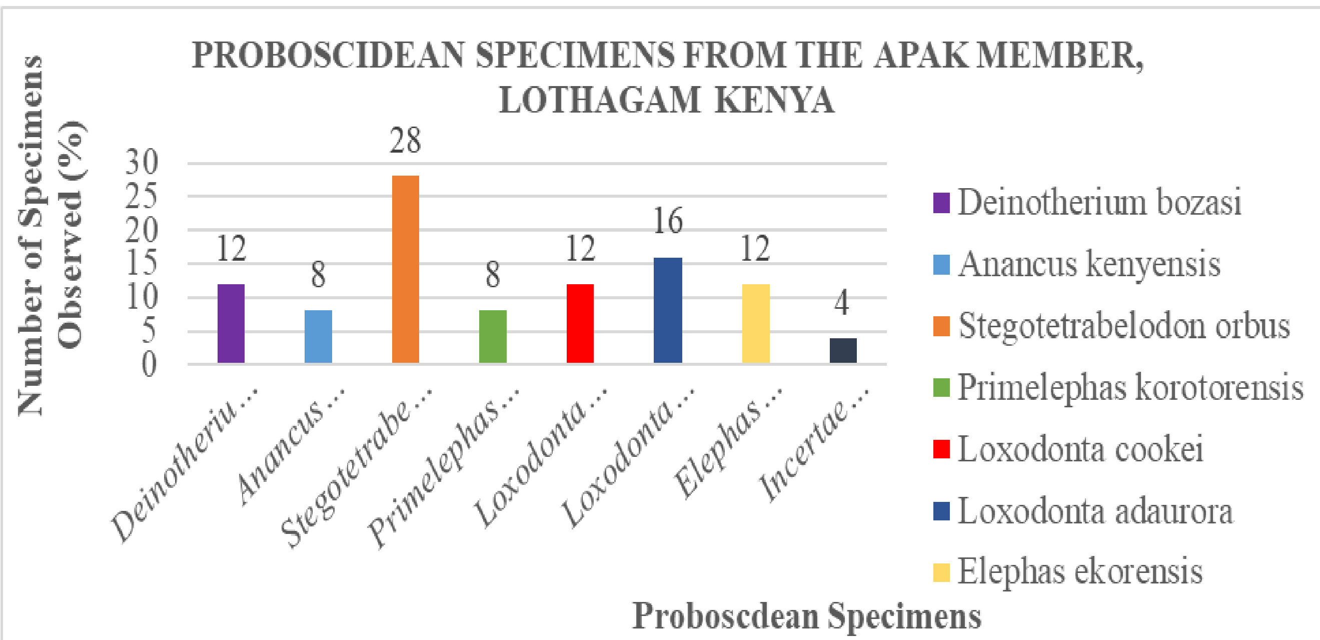

Figure 4.2: Showing proboscidean specimens observed in percentages % from the Apak Member at Lothagam, Kenya, based on the current study.

<u>**APPENDIX 5: APAK MEMBER PROBOSCIDEAN DATA SHEETS**</u>

SHOWING BOTH QUALITATIVE AND QUANTITATIVE INTERPRETATIONS

Specimen Data. All dimensions are in mm. "+" =missing or incomplete or worn; "x" =significant ridge, cingulum(id) or talon(id); "X" =incipient loph(id) or plate; L, length; W, width; H, height; LF, lamellar frequency (# plates per 100 mm); HI, hyposodonty index (H x 100/W); ET, enamel thickness.										
Taxon	Specimen #	Loc./Horiz. /Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
Loxodonta adaurora	KNM – LT 353 WT 153 67 K	Lothagam/ Nachukui Fm./ Apak or Kaiyumung Mb. /Pliocene	Broken skull (M3)	x 10 x	[Maglio, 1973: LF=3.9]	[Maglio, 1973 L=268.9]	[Maglio, 1973: W=107.2 (3)]	[Maglio, 1973: H=106.7]	[Maglio, 1973: HI=91]	[Maglio, 1973: ET=3.7-4.8]

-Occlusal surface was heavily worn.
- enamel has fine folding.
- Lamella folding's are still primitive, that is, not well developed.
- Despite the molar tooth being broken, it has a convex shape indicating it is an upper third molar.
- abundant cementum.
-the presence of *Loxodonta* sinus.

Comments slip

-Indicate that this specimen was loaned to Harvard University and was extensively damaged on its return journey. Presently this molar can only be assumed to be part of the skull.

A

B

Specimen Data. All dimensions are in mm. "+" =missing or incomplete or worn; "x" =significant ridge, cingulum(id) or talon(id); "X" =incipient loph(id) or plate; L, length; W, width; H, height; LF, lamellar frequency (# plates per 100 mm); HI, hyposodonty index (H x 100/W); ET, enamel thickness.										
Taxon	Specimen #	Loc./Horiz./Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
Stegotetrabelodon orbus	KNM – LT 354	Lothagam	r.M2-3;	r. M2=+5x	3.25	+160.5	92.6 (4)	Worn	--	5.5-7.0
	182 – 67K (Type)	? Apak/upper Nawata/late Miocene or early Pliocene	l. dentary with m2-3 and i2 (lower tusk)	r. M3=x6x	--	238.2	104.3 (3)	74.0 (4)	71	unworn
				l. m2=+5x	3.4	+166.6	90.0 (5)	worn	--	6.0
	Found in 1967			l. m3= x7x	3.0	276.7	92.5 (5)	88.0 (3)	--	--

--symphysis measures 390 mm from presymphysis to broken anterior

--dentary measures 570 mm posterior to break with symphysis

--symphysis strongly angled on dentary; angle of approach of tusk makes it impossible that its root could have continued into the dentary canal

--there is no actual observable connection between the symphysis+tusk piece and the dentary

--two mental foramina both under the absorbing alveolus for m1

--the root of ramus even with plate 3 of m3

--lower tusks eccentrically ovoid in cross-section with a trace of a slight lateral sulcus

--no apparent enamel band on the tusk

--tusk dimensions H=70 mm, W=58 mm

--m2 signs of accessory conules behind each plate

-strong postcingulid

--traces of cementum coating valley floors

--plates broadest basally and posteriorly

--m3 cementum thick, covering plate walls up to apices but not filling valleys

--plates primarily composed of four conelets

--accessory conules posterior to plates 1-2

--plates high centrally, no distinct median sulcus

--postcingulum distinct, formed of two strong pillars

--M2 with posterior accessory conules with plates 1-4

--transverse valleys V-shaped to sub-U-shaped

--plates pyramidal in lateral view

--M3 with posterior accessory conules with plates 1-2

--plates formed of five conelets

--conelets massive, especially basally

--V-shaped transverse valleys

--no median sulcus

A

B

C

D

E

F

G

H

Specimen Data. All dimensions are in mm. "+" =missing or incomplete or worn; "x" =significant ridge, cingulum(id) or talon(id); "X" =incipient loph(id) or plate; L, length; W, width; H, height; LF, lamellar frequency (# plates per 100 mm); HI, hyposodonty index (H x 100/W); ET, enamel thickness.										
Taxon	Specimen #	Loc./Horiz./Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
Stegotetrabelodon orbus	KNM – LT 355 208 – 67K	Lothagam Apak Member	A = r.m3 B = i.m3	A= x ½ 2 + B= x 2+	-- --	101.1 +91.0	84.9 (II) 81.0 (II)	Worn Worn	- -	5.5 5.5

A= tooth low crowned

-tooth critically worn and broken

- smooth folding of lamella

- plate 2 has no ac, which is not pronounced like in plate 1

- lots of cementum

- both A & B teeth are lower Lt & rt? 3 because of the concave shape of its occlusal surface.

B= tooth has less cementum

-enamel too thick

- Lamella has smooth folding.

- Tooth is worn out and broken

- The pc is not pronounced well in plate 1, but there is no ac. (image 1 is A & image 2 is B)

Specimen Data. All dimensions are in mm. "+" =missing or incomplete or worn; "x" =significant ridge, cingulum(id) or talon(id); "X" =incipient loph(id) or plate; L, length; W, width; H, height; LF, lamellar frequency (# plates per 100 mm); HI, hyposodonty index (H x 100/W); ET, enamel thickness.										
Taxon	Specimen #	Loc./Horiz. /Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
Deinotherium bozasi	KNM – LT 26345 92 WT 2357	Lothagam Upper Apak Member	Tooth fragments	-	-	-	-	-	-	-

- The tooth is critically broken and worn out.
- The tooth is in fragments.

Specimen Data. All dimensions are in mm. "+" =missing or incomplete or worn; "x" =significant ridge, cingulum(id) or talon(id); "X" =incipient loph(id) or plate; L, length; W, width; H, height; LF, lamellar frequency (# plates per 100 mm); HI, hyposodonty index (H x 100/W); ET, enamel thickness.										
Taxon	Specimen #	Loc./Horiz./Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
Stegotetrabelodon orbus	KNM – LT 365 55 – 68 K	Lothagam Horizon indet	r.dp3	+ 5 +	--	59.7	35.4 (4)	worn	-	2.4

-tooth critically worn

- low crowned
- tooth has a concave shape (lower molar).
- lamellar has fine folding.
- thinner enamel thickness.
- tooth has no cementum.

Specimen Data. All dimensions are in mm. "+" =missing or incomplete or worn; "x" =significant ridge, cingulum(id) or talon(id); "X" =incipient loph(id) or plate; L, length; W, width; H, height; LF, lamellar frequency (# plates per 100 mm); HI, hyposodonty index (H x 100/W); ET, enamel thickness.

Taxon	Specimen #	Loc./Horiz./ Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
Stegotetrabelodon orbus	KNM – LT 366 59 – 68K	Lothagam horizon indet	i.M2	x 5 x	4.0	173.1	83 (3)	worn	-	5.5

-Tooth is worn out

- Tooth has coarse folding

- pc is not well shown, ac is showing but not pronounced.

- transverse valley filled with cementum, in the two plates

- the enamel has smooth wearing.

Specimen Data. All dimensions are in mm. "+" =missing or incomplete or worn; "x" =significant ridge, cingulum(id) or talon(id); "X" =incipient loph(id) or plate; L, length; W, width; H, height; LF, lamellar frequency (# plates per 100 mm); HI, hyposodonty index (H x 100/W); ET, enamel thickness.

Taxon	Specimen #	Loc./Horiz./Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
Stegotetrabelodon orbus	KNM – LT 367 60 - 68K	Lothagam Horizon indet	r.M3	x 6x	3.0	231.7	101.3 (3)	worn	-	6.0

--tooth is heavily worn

-- coarse undulation of lamella

--presence of posterior accessory conules associated with plates 3, 4

--very thick enamel

--4-5 conelets per plate

--trace of cementum in transverse valleys

--postcingulum is simple, formed of one or two conelets.

--plates pyramidal in shape and massive

Specimen Data. All dimensions are in mm. "+" =missing or incomplete or worn; "x" =significant ridge, cingulum(id) or talon(id); "X" =incipient loph(id) or plate; L, length; W, width; H, height; LF, lamellar frequency (# plates per 100 mm); HI, hyposodonty index (H x 100/W); ET, enamel thickness.										
Taxon	Specimen #	Loc./Horiz./Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
Deinotherium bozasi	KNM – LT 23677 WT 1835	Lothagam Apak Member/ Kaiyumung Member	Rt. dp4 fragment	+ 3+	6	55.83	48.87 (III)	-	-	-

-Tooth was critically broken.
-The tooth has a high lamella frequency.

Specimen Data. All dimensions are in mm. "+" =missing or incomplete or worn; "x" =significant ridge, cingulum(id) or talon(id); "X" =incipient loph(id) or plate; L, length; W, width; H, height; LF, lamellar frequency (# plates per 100 mm); HI, hyposodonty index (H x 100/W); ET, enamel thickness.										
Taxon	Specimen #	Loc./Horiz./ Age (Ma)	Spec.	plates/loph(id) s	LF	L	W	H	H I	ET
Formerly *Primelephas gomphotheroides* Now, *Primelephas koroterensis*	KNM – LT 379 62 – 68k	Lothagam Apak Member	Molar plate	+ ½ 2 x	-	-		+40.0	-	5.4

-Plate is critically worn and broken

Specimen Data. All dimensions are in mm. "+" =missing or incomplete or worn; "x" =significant ridge, cingulum(id) or talon(id); "X" =incipient loph(id) or plate; L, length; W, width; H, height; LF, lamellar frequency (# plates per 100 mm); HI, hyposodonty index (H x 100/W); ET, enamel thickness.										
Taxon	Specimen #	Loc./Horiz./Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
Deinotherium bozasi	KNM – LT 23806 WT 1886	Lothagam Apak Member	Molar frags	-	-	-	-	-	-	-

- Tooth critically broken.
- The tooth is in fragments.

Specimen Data. All dimensions are in mm. "+" =missing or incomplete or worn; "x" =significant ridge, cingulum(id) or talon(id); "X" =incipient loph(id) or plate; L, length; W, width; H, height; LF, lamellar frequency (# plates per 100 mm); HI, hyposodonty index (H x 100/W); ET, enamel thickness.

Taxon	Specimen #	Loc./Horiz./Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
Loxodonta sp.cf *Loxodonta cookei*	KNM – LT 23786 WT 1692	Lothagam IC Upper Apak Member, Nachukui Formation	r.m3 or i.M3	+ ½ 3 x	4	+150.4	109.7 (III)	worn	--	5.7 - 6.1

- very large specimen/huge conulets, thick enamel.

- 3-4 conulets per plate or more.

- the presence of ac and pc in plate two and partly in plate one.

-definite marked midline expansion of central pillar suggesting nascent Loxodont sinus, probably incorporating anterior accessory conules into enamel wear figure, plate II.

- enamel unfolded.

- cementum invested in transverse valleys.

- too primitive to be *L. exoptata.*

-crown taper posteriorly to a point.

- only a posterior fragment of the plate IV remains broken anteriorly.

Specimen Data. All dimensions are in mm. "+" =missing or incomplete or worn; "x" =significant ridge, cingulum(id) or talon(id); "X" =incipient loph(id) or plate; L, length; W, width; H, height; LF, lamellar frequency (# plates per 100 mm); HI, hyposodonty index (H x 100/W); ET, enamel thickness.

Taxon	Specimen #	Loc./Horiz./ Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
formerly *Loxodonta aff. exoptata* But now, *Loxodanta cookei*	KNM – LT 23794 WT - 1649	Lothagam Lower Apak Mb. (South) early Pliocene	Partial Right M3.	+ ½ 5 x	4.5	154.0	93.7 (V)	worn	-	4.3 – 4.7

-Tassy (2003) identified molar as *aff*. *Loxodonta exoptata*, prior to recognizing *L. cookei* as a species (Sanders, 2007).

- Transverse valley is open and filled with cementum.

- Plates parallel-sided.

Propeller–shaped arms and prominent central sinus in each enamel wear figure; evident that, anteriorly, anterior and posterior expansion of enamel touch in the midline.

- Plates parallel

- Transverse valley u-shaped at the base.

- 5 – 7 conelets per plate.

- Enamel is roughly irregularly undulated in plates and coarsely folded medially but smooth laterally

Specimen Data. All dimensions are in mm. "+" =missing or incomplete or worn; "x" =significant ridge, cingulum(id) or talon(id); "X" =incipient loph(id) or plate; L, length; W, width; H, height; LF, lamellar frequency (# plates per 100 mm); HI, hyposodonty index (H x 100/W); ET, enamel thickness.										
Taxon	Specimen #	Loc./Horiz./Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
Elephas cf. ekorensis	KNM – LT 23795 WT 1613'91	Lothagam Apak Member	i.M1	+ 3 x (precingulum and first three plates)	6	+75.3+	67.6 (3)	worn	-	3.1

-Tooth has a convex occlusal surface showing that it is an upper left molar tooth.

- Plate 1 has a tiny ac 1 and pc 1; plates 2 – 3 have increasingly more significant pc 2 – pc3.

- Enamel thickness is modest.

-The tooth has pronounced ac on plate 2 and lacks pc on other plates.

- The tooth has coarse folding or unclulation of enamel loops.

- Tassy (2003) identified this specimen as *Elephas cf. ekorensis*.

- Weak or absent expression of anterior accessory conules and presence of posterior accessory conules behind each plate signal that this is likely not a molar of Loxodonta, and it does not seem archaic enough in morphology to be a *Stegotetrabelodont* or *Primelephas.*

- cementum is present in the transverse valleys between plates.

- in the photo, the anterior is at the bottom of the picture.

Specimen Data. All dimensions are in mm. "+" =missing or incomplete or worn; "x" =significant ridge, cingulum(id) or talon(id); "X" =incipient loph(id) or plate; L, length; W, width; H, height; LF, lamellar frequency (# plates per 100 mm); HI, hyposodonty index (H x 100/W); ET, enamel thickness.

Taxon	Specimen #	Loc./Horiz./Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
Loxodonta adaurora	KNM – LT 23797 WT 1842'91	Lothagam Apak Member	Part molar frag	+ 5 x	6	105.09	70.68 (1)	worn	--	--

-Tooth is critically worn & broken.

- Tooth has both ac & pc

- Loxodonta sinus, well defined.

- plates are almost packed together.

- tooth has a high lamella frequency.

-Tooth appears to be a lower molar due to the concave shape.

Specimen Data. All dimensions are in mm. "+" =missing or incomplete or worn; "x" =significant ridge, cingulum(id) or talon(id); "X" =incipient loph(id) or plate; L, length; W, width; H, height; LF, lamellar frequency (# plates per 100 mm); HI, hyposodonty index (H x 100/W); ET, enamel thickness.										
Taxon	Specimen #	Loc./Horiz./Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
Elephas ekorensis	KNM – LT 23799 WT - 1840	Lothagam Apak Member	Molar & tusk frags	+ 4 x	6.0	+61.8	51.2 (3)	worn	-	`

-Tooth has thin & fine enamel folding.

- lots of cementum.

- appears to be upper molar due to the convex shape of the occlusal surface.

- no clear ac or pc.

- tooth broken & critically worn.

Specimen Data. All dimensions are in mm. "+" =missing or incomplete or worn; "x" =significant ridge, cingulum(id) or talon(id); "X" =incipient lop(id) or plate; L, length; W, width; H, height; LF, lamellar frequency (# plates per 100 mm); HI, hyposodonty index (H x 100/W); ET, enamel thickness.										
Taxon	Specimen #	Loc./Horiz./Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
Elephas ekorensis Comment slip (Bill Sanders) – probably *Loxodonta adaurora*	KNM – LT 26320 WT 2016	Lothagam upper Apak Member just below basalt coarse grey sand	Left dentary with dp4 and erupting m1	A= x 8 x B= x 7 x	8 5.5	121.7 --	59.0 (6) --	Worn Worn	-- --	2 --

-All plates in wear in dp4

- high crowned tooth.

- posterior accessory conule 1-7

- anterior accessory conules 1- 6

- coarse folding of enamel

- plate 1 is subdivided in the midline

- Tooth has a concave shape meaning it's a lower molar tooth.

- Transverse valley is filled with cementum.

- compare with specimens S. Turkwel, Kanapoi.

Specimen Data. All dimensions are in mm. "+" =missing or incomplete or worn; "x" =significant ridge, cingulum(id) or talon(id); "X" =incipient loph(id) or plate; L, length; W, width; H, height; LF, lamellar frequency (# plates per 100 mm); HI, hyposodonty index (H x 100/W); ET, enamel thickness.										
Taxon	Specimen #	Loc./Horiz./Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
Loxodonta cookei	KNM – LT 26321 WT 2027	Lothagam middle Apak Member	I?m2	+ 4 x	--	+71.2	72.2 (4)	worn	-	3.7

-Molar tooth is highly worn.

- Molar tooth has coarse folding.

- ac and pc touch each other.

-Transverse valley is filled with cementum.

- The broken molar piece has a concave shape, meaning it's a lower molar tooth.

Specimen Data. All dimensions are in mm. "+" =missing or incomplete or worn; "x" =significant ridge, cingulum(id) or talon(id); "X" =incipient loph(id) or plate; L, length; W, width; H, height; LF, lamellar frequency (# plates per 100 mm); HI, hyposodonty index (H x 100/W); ET, enamel thickness.										
Taxon	Specimen #	Loc./Horiz./Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
Incertae sedis B	KNM – LT 26323 WT 2042	Lothagam formation – Nachukui Level – middle Apak Member	? upper molar	+ 4 x	4	+129.0	+90.3 (III)	worn	-	3.0 – 3.4

-The tooth seems to be a lower right molar tooth because of the concave shape and the curving inside.

- it's the last m3 because of the almost sharp posterior end.

- plate 1 shows the presence of a pc and no ac.

- molar tooth has fine folding.

-tooth, worn out and has less cementum.

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Taxon	Specimen #	Loc./Horiz./Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
? *Stegotetrabelodon orbus*	KNM - LT 26337	Lothagam Nachukui Apak Member	Molar frags	A= + 2 +	-	56.5	-	-	-	-
				B= + 2+	-	43.5	-	-	-	-
	WT 2632			C= +2 +	-	38.8	-	-	-	-

-Tooth broken.

- has traces of cementum.

Specimen Data. All dimensions are in mm. "+" =missing or incomplete or worn; "x" =significant ridge, cingulum(id) or talon(id); "X" =incipient loph(id) or plate; L, length; W, width; H, height; LF, lamellar frequency (# plates per 100 mm); HI, hyposodonty index (H x 100/W); ET, enamel thickness.										
Taxon	Specimen #	Loc./Horiz./Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
Loxodonta adaurora	KNM – LT 26340 WT 2705	Lothagam Nachukui Formation Kaiyumung/Apak Member	Tooth frags	(A)+ 2 x	-	34.3	34.5 (2)	-	-	2.0
				(B)+ 2 x	-	27.7	43.3 (2)	-	-	-
				(C)+ 2 x	-	22.7	45.0 (2)	-	-	-

A – Tooth broken & worn out.

- Tooth has no cementum
- The tooth is *Loxodonta adaurora* because of the *Loxodonta* sinus
- plate (1) has both ac and pc

B - tooth extensively worn out.

-there is evidence of cementum.

C – tooth is extensively broken.

-appears to be the erupting part of the molar tooth where plates are not yet developed.

A

B

C

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Taxon	Specimen #	Loc./Horiz./Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
Elephas ekorensis	KNM – LT 26581 WT 2581	Lothagam Nachukui formation level – Kaiyumung/ Apak	Broken M1	+ 7 x	4.0	+109.7	47.7 (3)	worn	-	-

-Tooth is extensively worn

-Tooth is smaller than m3 (s).

-Tooth has fine lamella folding.

- Plate size is small.

- upper molar due to convex occlusal surface

- The plates are closely packed together.

- Thin enameled.

- Presence of cementum.

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Taxon	Specimen #	Loc./Horiz. /Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
Anancus kenyensis	KNM – LT 341 41- 67 K	Lothagam Apak Member	Molar frags (a-c) A – Rt m3 B-Rt m3 C –Rt m3	A = + 2 x B = +2 x C = + 4 x	4.0 4.0 4.0	58.9 108.2 106.0	50.0 (1) 62.8 (2) 69.31 (1)	Worn Worn Worn	- - -	4.0 4.0 4.0

-tooth is critically worn & broken.

- tooth is primitive; the molars are said to be enormously constructed, with little evidence of accessory conules.

- tooth has no definite plate with complete lamella

- the third molar in the picture is not Anancus but is an elephant molar

Specimen Data. All dimensions are in mm. "+" =missing or incomplete or worn; "x" =significant ridge, cingulum(id) or talon(id); "X" =incipient loph(id) or plate; L, length; W, width; H, height; LF, lamellar frequency (# plates per 100 mm); HI, hyposodonty index (H x 100/W); ET, enamel thickness.										
Taxon	Specimen #	Loc./Horiz./Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
Primelephas koroterensis	KNM – LT 363	Lothagam Apak Member	Molar plate?M2	+ 3 x	-	+81.0	84.4 (1)	55	-	-

-Tooth is broken.

- Just a plate and an extended x/end.

-lots of cementum.

-enamel thickness cannot be measured (no point of measurement).

Specimen Data. All dimensions are in mm. "+" =missing or incomplete or worn; "x" =significant ridge, cingulum(id) or talon(id); "X" =incipient loph(id) or plate; L, length; W, width; H, height; LF, lamellar frequency (# plates per 100 mm); HI, hyposodonty index (H x 100/W); ET, enamel thickness.										
Taxon	Specimen #	Loc./Horiz. /Age (Ma)	Spec.	plates/loph(id)s	LF	L	W	H	HI	ET
Anancus kenyensis	An anterior portion of lt. lower molar	Lothagam IC Upper Apak Member	KNM – LT 23790 WT 1797'91	+ 2 x	4.0	+63.4	60.2 (II)	worn	-	-

-Unlimited accessory conules

- tooth is severally broken, and very hard to describe other items such as lamellar.

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NATIONAL COMMISSION FOR SCIENCE, TECHNOLOGY & INNOVATION

Ref No: **841270**

Date of Issue: **24/October/2021**

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