ADDIS ABABA UNIVERSITY

COLLEGE OF NATURAL AND COMPUTATIONAL SCIENCES

PALEOANTHROPOLOGY AND PALEOENVIRONMENT PROGRAM

‘‘RECONSTRUCTING THE DIETARY PREFERENCE AND THE PALEOECOLOGY OF THE FOSSIL FAMILY RHINOCEROTIDAE (MAMMALIA: PERISSODACTYLA) FROM THE HOMINID BEARING PLIOCENE HADAR FORMATION OF ETHIOPIA USING EXTENDED DENTAL MESOWEAR ANALYSIS’’

BY

GETAHUN TEKLE YEMANEBIRIHAN

A thesis submitted to college of natural and computational sciences Paleoanthropology and Paleoenvironment program of Addis Ababa University in Partial fulfillment of the degree of Master of Science in Paleoanthropology.

Advisor

MULUGETA FESEHA (Ph.D.)

Date

Addis Ababa, Ethiopia

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Approved by Examining Committee

___________________________ (Examiner) ______________________

__________________________(Examiner) ______________________

___________________________(Advisor) ______________________

___________________________ (Chairman) ______________________

DECLARATION

I, hereby, declare that the thesis entitled ‘’Reconstructing the dietary preference and the paleoecology of the fossil family rhinocerotidae (mammalia: perissodactyla) from the hominid bearing Pliocene Hadar formation of Ethiopia using extended dental mesowear analysis’’ is my original work and has not been presented for a degree in any other university, and that all sources of material used for the thesis have been duly acknowledged.

Name: Getahun Tekle Yemanebirihan

Signature:

Date of submission June 21, 2023

This thesis has been submitted for examination with my approval as the research advisor.

Name Dr. Mulugeta Feseha

Signature ____________________

Date _________________________

Addis Ababa, Ethiopia

ACKNOWLEDGMENT

I would like to express my sincere gratitude to my thesis supervisor Dr. Mulugeta Feseha, Associate Professor, Paleoanthropology and Paleoenvironment Program, College of Natural Sciences, Addis Ababa University. His patience, enthusiasm, co-operations and suggestions made me to publish my thesis in its current form. His brilliant, skillful supervision enriched this study higher than my expectation. I could not remain any more without giving heartfelt thanks to Dr. Mulugeta Feseha for his painstaking supervision throughout the study period.

I would like to express my deepest gratitude to Dr. Agazi Negash and Dr. Tekie whose sincerity and encouragement that I will never forget. They have been an inspiration as I hurdled through the path of this Master's degree. They are the true definition of leaders and the ultimate role models.

I would also like to thanks to all my respected teachers in Paleoanthropology and Paleoenvironment program and all the other members of departments who directly and indirectly provided me inspirations and valuable suggestion during the course of this study. Ethiopian Heritage Authority, National Museum of Ethiopia for providing me this Master's scholarship.

This thesis would not have been possible without Mr. Tomas Getachew, Mr. Sahilesilassie Melaku, Blade Engidaw (Ph.D.), Temesgen Leta and Enquye Negash (Ph.D.) whose guidance from the initial step in research enabled me to develop an understanding of the subject. I am thankful for the extraordinary experiences they offered me and for providing me all the opportunities to grow professionally.

I am grateful for my parents, friends and colleagues, whose constant love and support keep me motivated and confident. My accomplishments and success are because they believed in me.

This thesis work is dedicated to Dr. Solomon Yirga.

TABLE OF CONTENTS **PAGE**

APPENDIX

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Rhinos are the largest, taxonomically diverse and the most successful perissodactyl group on earth. The fossiliferous Pliocene Hadar Formation has yielded abundant fossil faunal specimens including two rhino lineages and hominins like the famous *Australopithecus afarensis*. The two rhino lineages are the browsing *Diceros* and the grazing *Ceratotherium*.

Dental mesowear analysis is a method used to infer the dietary category of herbivore mammals as browser, grazer or mixed feeder, recorded over a long time based on the facet developed due to attrition (tooth on tooth contact) and abrasion (tooth on exogenous materials, mostly food contact) on the ectoloph occlusal surface of the tooth. By analyzing the fossil tooth specimens it is possible to reconstruct the diet and dietary ecology specific group of individual as well as paleocommunities in that ecosystem.

In this study the maxillary P2-M2 of *Dicerose praecox* and *Ceratotherium mauritanicum*, were analyzed using the extended mesowear method of rhino's with objective of reconstructing the paleodietary adaptation of the Family rhinocerotidae to study and understand their paleoecology. The mesowear result indicate that *Dicerose praecox* is a browser probably feed on varieties of leaves, shoots, tree bark, or fruits whereas *Ceratotherium mauritanicum* is grazer that feed on grasses and other low-growing vegetation. A wide range research conducted on the extant representative of the two lineages, *Diceros bicornis* (The African black rhino) and *Ceratotherium simum* (The African white rhino) found similar result with the present study indicate their feeding behavior is still preserved.

Australopithecus afarensis that inhibited in a similar environment with other contemporaneous mammalian groups is believed to have experienced the same climatic and environmental conditions. Therefore; the inferred paleoenviromental condition of the two lineages also define other mammals including hominins that lived the same environment and similar time period.

Key words: *Ceratotherium mauritanicum*, *Dicerose praecox*, Diet, Mesowear, Paleoecology Paleoenviroment,

CHAPTER ONE INTRODUCTION

1.1. BACKGROUND

The Family rhinocerotidae together with *Amynodonts* and *Hyracodonts* all diverged from Hyrachyus in the late Eocene to form a super family Rhinocerotoidae. During Oligocene the Family Rhinocerotidae appeared to be the dominant large mammal in North America. In Europe on the other hand lineages ranging from medium to large size including semi-aquatic rhinocerotids began to emerge (Prothero et.al, 1989).

During the early Miocene like other African animal groups, Family Rhinocerotidae showed significant diversity especially between 18 Ma and 15 Ma, and before 7 Ma, though there are inadequate records between these periods and before 18 Ma (Werdelin & Sanders, 2010). The family was represented by six lineages that correspond to the sub-families (*Aceratheriinae*, *Dicerorhininae*, *Brachypotheriinae*, *Chilotheriinae Iranotheriinae* and *Dicerotiinae*) (Geurin, 2003).

However due to a crisis called the Mediterranean salinity event, the cyclic desiccation of Mediterranean Sea, and the resulted climatic change which took place in the lower Miocene led to the extinction of large group of animals. Following the crisis at the Miocene Pliocene boundary in North America almost the entire rhino species extinct whereas, in Eurasia two lineages (rhinocerotine and dicerorhinus) and in Africa one lineage, dicerotine were survived (Prothero et.al, 1989).

African Plio-Pleistocene is comprised of a unique collection rhinocerotids including dicerotine, exclusively an African tribe represented by two extant African rhinos, *Diceros bicornis* and *Ceratotherium simum* and other exotic lineages (Prothero et.al, 1989). *Ceratotherium*, grazer and *Dicerose*, browser are evolved from the late Miocene species *Ceratotherium neumayri*, probably a mixed feeder and the likely ancestor of both of them, as it is both morphologically and ecologically intermediate between the two lineages (Geraads,2005).

The modern species of *Dicerose*, *D.bicornis* originated from African paradicerose during the Pliocene (4 Ma). It is the most stable and long-lived species of Africa. With the exception of northern Africa, it spread all over sub-Saharan Africa whereas, *Ceratotherium simum* evolved from *Ceratotherium praecox* (immediate ancestor to *ceratotherium simum*) between 4 and 3 Ma (Hooijer, 2013).

Like other African Plio-Pleistocene mammalian localities fossil representatives of the two extant rhino lineages were once lived at the Hadar formation, Ethiopia (Geraads, 2005). Genus *Ceratotherium*, represented by *Ceratotherium mauritanicum*, the first fossil rhino species ever named in Africa and genus *Dicerose*, represented by *Dicerose praecox* co-occurred in the Pliocene Hadar Formation (Geraads, 2005).

There are five extant species of rhinos found mainly in two continents, Africa and Asia despite they are either threatened or close to extinction. *Dicerorhinus sumatrensis* (a two horned rhino) found in Sumatra and Malaysian peninsula, *Rhinoceros sondicus* and *Rhinoceros unicornis* both are single horned rhino species found in southeastern Asia and the square lipped *Ceratotherium simum* (living African white rhinocerose) and the hook-lipped *Diceros bicornis* (the living African black rhinocerose) are found in Africa (Geraads et.al., 2005).

The two African living rhinocereotids have lived for about 4 to 3 million years without having significant morphological change but inhibiting different biomes. *D.bicornis*, browser prefer to live in wooded or bushy savanna or open woodland and *Ceratotherium simum*, grazer prefer open savanna or grassland (Guerin, 2003).

Generally, they are the largest, taxonomically diverse and one of the most successful perissodactyl group on the earth (Prothero et. al, 1989).

In order to better understand the natural variability and evolution of Palaeoecosystems and -climates, fossil faunal remains can be used as tools for reconstructing Palaeoenvironmental parameters (Kahlke & Kaiser, 2011).

Mammalian teeth typically maintain information enough to make specific or general identification because teeth are regularly preserved in fossil record due to the exceptional durability of enamel. Therefore, studying large sample sizes leading to increased confidence in interpretations and chances to observe patterns within and between populations, is vital to interpret Paleodiet and Paleoenvironments (Green and Croft, 2018).

Fossil herbivore teeth is usually used in reconstructing the paleodiet of extinct species (Fortelius & Solounias, 2000) because studying their paleodiets can provide important evidence about past ecology (Negash, 2020). However, the methods used so far to study fossil specimens to infer paleodiet so that to reconstruct paleoecology have been painstaking, expensive and consume too much time, thus only small number of species from limited localities are analyzed. Therefore, in order to overcome the shortcomings of previous techniques a new method, mesowear, was introduced. This method is relatively more efficient, requires less resources (inexpensive), enable to study and analyze large number of samples with minimal expenditure of time (Fortelius & Solounias, 2000) and it is nondestructive (Green and Croft, 2018).

Mesowear method is rapid and simple to record, depending on the method used, scoring might be more or less simple, although even the most complicated schemes only need a pair of calipers, a digital camera, and a laptop computer so, specimens can be scored directly in museum collections, allowing for the inexpensive acquisition of large samples. It is also taxon independent due to the fact that the wear being assessed is largely the result of the ingested materials, which tend to produce similar dental features in different groups that feed on similar ingesta (Green and Croft, 2018).

The classical mesowear method analysis is done by observing the morphological features on the second maxillary molar with the naked eye or hand lens, if necessary. Occlusal relief (high or low) and cusp shapes (Sharp, Round or Blunt) are the two variables in mesowear scoring (Fortelius & Solounias, 2000).

Mesowear patterns are analyzed based on facet developed on tooth due to attrition (tooth on tooth contact) and abrasion (tooth on exogenous materials, mostly food contact) and from the observation of wear patterns it is possible to infer dietary category of herbivores into browser, grazer, and mixed feeder. Browsers generally show attritive wear patterns whereas grazers show abrasive wear patterns (Fortelius & Solounias, 2000).

For the present study mesowear method were applied on the maxillary P2-M2 and only focused on the rhinocerotid fossil specimens collected from the Hadar Formation that aimed at understanding their general dietary adaptation so that to reconstruct their paleoecology.

1.2. LOCATION OF THE STUDY AREA

The fossiliferous Pliocene Hadar site is located in Afar regional state of Ethiopia (11°10°N and 40°35°E) along the Awash River in Afar depression located at the northeast of Addis Ababa, Ethiopia (Taieb et. al., 1976, Johanson et. al., 1982).

The name Hadar comes from the large tributary of the Awash River that cuts through the central exposure of the area. The area extends to the east Hurda Wadi, south to the Awash River, west to Gona Wadi and north to Ledi Wadi (Johanson et. al., 1982).

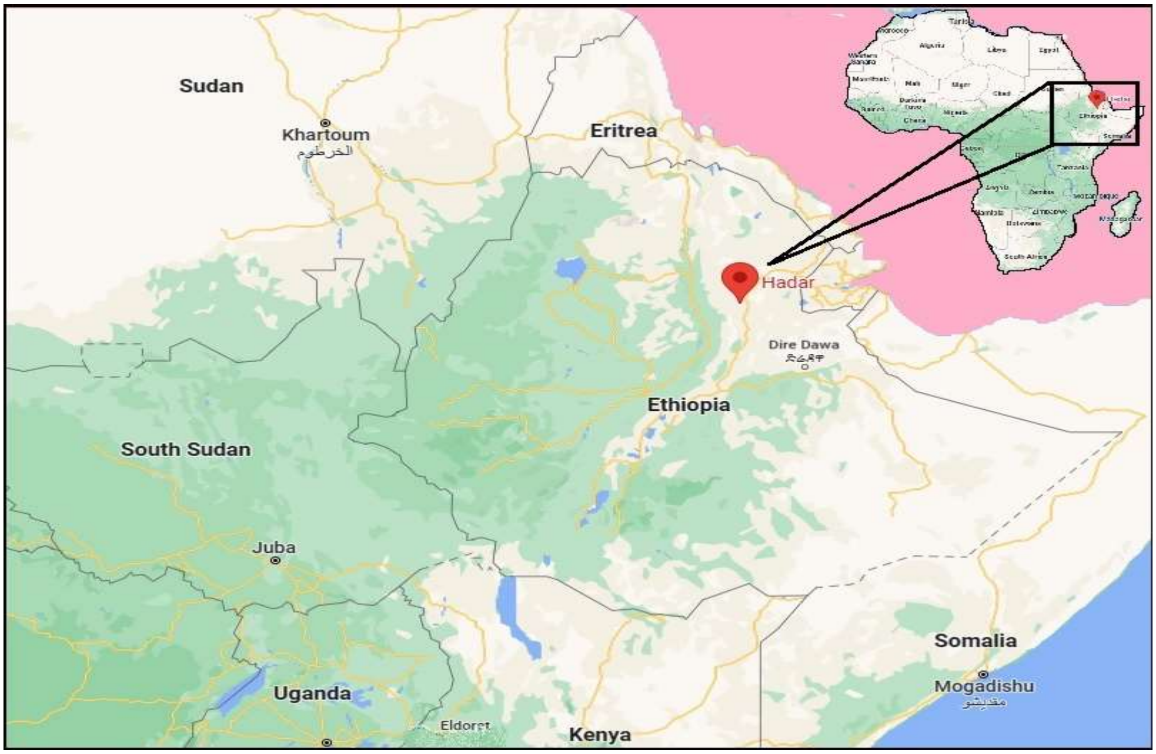


Figure 1. Location map of the Hadar paleoanthropological site, Ethiopia (source: Google Maps).

The Pliocene Hadar Formation is comprised of fluvio-lacustrine sediments (~155 m) maintaining detailed geologic events that are rich in paleontological records and a high-resolution record of environmental conditions between 3.45Ma to 2.9 Ma that can provide solid foundation to understand the Paleoenvironment of Australopithecus afarensis and the overlying Pliocene Pleistocene Busidima formation separated from the Hadar Formation by regional angular unconformity also provides evidence of the genus Homo and Oldowan stone tools (Campisano & Feibel, 2008).

Hadar is located in arid environment with mean annual rain fall of 500mm, mean annual temperature 26.6°C and evapotranspiration of 1,750 mm/yr. (Bonnefille, 2004). The vegetation is dominated by Acacia/ Commiphora steppe and shrub lands, big trees of riparian vegetation found along the Awash River and Acacia wood land that dominate the plateau and the rocky slopes of the escarpment (Bonnefille, 1987 and 2004).

Several rivers, streams and gullies and other systems that all drain into the Awash River are responsible for erosion of rock materials to create badlands so that to expose the Pliocene Pliestocene sediments underneath (Campisano, 2007).

1.3. HISTORY OF RESEARCH AT HADAR

Due to its remoteness as well as hostile indigenous tribes the Afar triangle was remained unexplored. But in the 1960s Maurice Taieb conducted research on the geological evolution of the Awash River and through continues field works focusing on sedimentary and stratigraphic investigations, he discovered a Pliocene-Pleistocene series of fossiliferous deposits (Johanson et. al., 1982).

In 1972, with the support of the Ethiopian government he set up another expedition to Afar by inviting Taieb D.C. Johanson, Y. Coppens, and J.E. Kalb with the goal to conduct geological and paleontological survey (Johanson et. al., 1982) and evaluate its potential to conduct further investigation (Johanson 2016). This marked the establishment of the International Afar Research Expedition (I.A.R.E.) to undertake expanded field exploration in the Afar (Johanson et. al., 1982).

In 1973, they conducted the first major expedition after they received grants from various sources so that they collected and mapped close to 89 localities in Hadar and the first hominid fossils were located (Johanson et. al., 1982). The expedition was focused on sites where there were deep and exposed fossil rich sediments (Johanson, 2016).

In 1974, they continued their survey at Hadar and found the first dental remains and associated jaws. In the same year, Johansson and Tom Gray discovered a 40% complete hominid fossil skeleton later named as *Australopithecus afarensis* (Lucy) (Johanson et. al., 1982).

In 1975, the team recovered more than 200 hominin fossil specimens from A.L. 333 (Johanson, 2016). From 1975 until the fall of 1981 a geologist John Kalb established Rift Valley Research Mission in Ethiopia and in collaboration with American and Ethiopian scholars conducted anthropological, archaeological, and geological investigation in the middle Awash area (Lewin, 1983).

From 1981 to 1990 the field expedition was halted because of the political instabilities in Ethiopia. Beginning from 1990 Hadar Research Project (HRP) started the expedition again with the goal to answer basic questions regarding the geology, paleontology, and paleoanthropology of the Hadar Formation and continuing until today (Johanson, 2016).

1.4. STATEMENT OF THE PROBLEM

Although paleoecology of herbivores can be reconstructed from the records on the fossil specimens and their geological context, fossil herbivore teeth is a widely used tool because there is close evolutionary relationship amongst each other which enable them to acquire traits that are easily understandable (Fortelius and Solounias, 2000).

Dental wear patterns provide evidence about the type of foods eaten by the animal. Tooth is therefore, an ideal source for the reconstruction of ecology, physiology and life history of extinct as well as living animals (Bohmer and Rossner, 2018) and enables to understand the relationship between growth, function and evolution (Fortilius, 1985).

In terms of Human evolutionary study analysis of the different paleoecological patterns recorded on the fossil specimens like habitat reconstruction, identification of temporal and spatial habitat and species changes can provide us contextual meanings important to understand the evolution of hominins (Reed, 2008).

Many of the previous attempts of paleoecological studies on the proposed areas (Example; Bedaso et al., 2012, Grine et al., 2006, Martin et al., 2018, Reed, 2008, Wynn et al., 2013,) were carried out either using a single method only or on a small sample size of specific taxa that may not provide the most reliable results and may lead to misinterpretations. Therefore, "Using multiple approaches for addressing a question proves to be useful in paleontology because it allows for yielding more robust results and broader insights." (Hullot et al., 2021, p. 2).

Unlike the previous methods, dental mesowear analysis proposed by (Fortelius and Solounias, 2000) applies a simple procedure to analyze large number of samples from multiple localities in a short period of time and the result obtained from the analysis is more reliable enough to make inference.

Despite the ecological necessities of extant species and their fossil representative showing some degree of similarities, analysis conducted using varies paleoecological reconstructing methods indicate that lineages show temporal variation in their diets and habitats (Boisserie et al., 2008). As a result, what is observed in a few years' time and in a particular place may not remain similar for thousands or millions of years (Ackermans, 2020). Therefore, application of varies independent methods to reconstruct past ecology using the records on the fossil assemblages can provide important evidence either supporting or disproving the existing hypotheses about ecological evolution (Boisserie, et al., 2008).

According to Taylor et al., 2013 "The adaptive value of the wear-induced tooth morphology in rhinos has not been widely studied, and data on individual cusp and tooth positions have rarely been published." Although research have been undertaken using a wide variety of methods on the fossil specimens from Hadar Formations with the aim of reconstructing the paleoecology, application of mesowear method especially on rhino fossil specimens is very rare.

Therefore, the proposed study will try to answer basic questions related to the paleoecology of the *family rhinocerotidae* in Hadar Formation that will provide additional evidence to other studies of paleoecological proxies.

1.5. OBJECTIVES

1.5.1. GENERAL OBJECTIVE:

The overall objective of this study is to examine and understand the dietary adaptation of fossil specimens of the *Family Rhinocerotidae* from Hadar Formation (Lower Awash Valley) to reconstruct their paleoecology.

1.5.2. SPECIFIC OBJECTIVES:

- Investigate the mesowear pattern of rhino fossil species through comparisons with the existing database composed of living species whose behaviors are well known.
- Determine the dietary preference of the two lineages (*Diceros* and *Ceratotherium*) and characterize them according to their dietary category as grazer, browser or mixed feeder.
- Investigate the changes in their dietary adaptations of the two rhino lineages across the different members and sub-members of the Hadar Formation and their relation to human evolution.
- Compare the results and interpretations of this study with previous researches.

1.6. SIGNIFICANCE OF THE STUDY

Local habitats and early human evolution in Africa are thought to have been significantly impacted by global temperature change during the Plio-Pleistocene (Bonfille, 1984). The fossiliferous Pliocene hominin-bearing sediments of the Hadar Formation maintain a record that revealed hominin habitat and environmental changes between 3.45Ma and 2.94Ma (Campisano, 2007*). A. afarensis* was recovered from the entire members of the Hadar Formation which suggests that the species had survived in various biomes and environmental change had no significant effect to adapt different environmental conditions (Bonfille 2004).

Other mammalian fossil specimens found associated with hominin specimens in the same deposits are the most commonly used data to answer basic questions related to evolutionary paleoecology (Reed, 2012). For instance, understanding the Paleodietary preference of herbivores and their dietary evolution provide us information to better understand the changing environmental conditions (Bonfille, 2004).

Understanding the paleoecology of early hominins is not only reconstructing their habitat but also understanding the ecological context before and after speciation and interaction with biotic and abiotic elements of the ecosystem. Therefore, by examining the contemporaneous animals and plants it is possible to reconstruct the general ecological context and evolutionary drivers of patterns in early hominin diets. The information about diet will be used to observe the temporal and spatial change in the Paleoenvironmental conditions that help us to better understand hominin environments and their impact on early hominin evolutionary speciation, migration, or extinction. Though the two lineages of rhinocerotids are not uniformly distributed across each member of the Pliocene Hadar Formation, they provide us an opportunity to understand the relationship between the environment and hominin evolution.

1.8. LIMITATIONS OF THE STUDY

It is not easy to find fossil specimens in large numbers because not all skeletal parts are preserved as fossils as they are damaged either by the geologic, taphonomic or other processes. Therefore, smaller number of sample size is the first and the most limiting factor.

Complete skeletal specimens are the most important tools than isolated or fragmentary parts as they are suitable to confidently identify taxonomic levels but fossils are usually found in isolated form, which is another limiting factor in the study of fossil specimens using their functional morphologies. There were unequal sample sizes in each cusp and tooth position as a result of damaged/broken cusps and exclusion of wear stages.

Mesowear develops over an animal’s lifetime (from months to years) and it reflects the average diet of a particular species from a particular location in space and time. It does not determine the animal’s last meal so that it cannot detect transitions in diet on shorter time scales, lacks detecting seasonal changes. It only determines how relatively abrasive is the food eaten by the animal therefore it reflects the role of attrition and abrasion for tooth wear development with the primary goal of categorizing animals as browsers, grazers or mixed feeders (Fortelius and Solounias 2000).

1.7. ORGANIZATION OF THE THESIS

This Thesis consists of six chapters. Chapter one includes the background information, research history in the site and general information of the study area in statement of the problem, the objectives the study, significance of the study, and limitations of the study. The Second Chapter is the literature review part and consists of the evolutionary history of the family rhinocerotids, dental evidence of dietary adaptation, as well as the geology, previous paleoecological studies and faunal assemblages of the Hadar Formation. Materials used for the study and methods applied for the analysis are the main topics in Chapter Three. Chapter Four consists of the results obtained from the analysis. Detailed discussion and interpretation based on the results obtained and comparison with similar previous studies and theories are included in Chapter Five. Finally in Chapter Six conclusion based on interpretation of the results and recommendation for future studies are included.

CHAPTERTWO LITERATURE REVIEW

2.1. EVOLUTIONARY HISTORY OF FAMILY RHINOCEROTIDAE

Historically rhinos are one of the most successful *perrissodactyls* group on the earth's crust (Prothero et. al., 1989). *Family rhinocerotidae* together with Tapiridae and Equidae make up the order perissodactyla (Tougard et al., 2001). In the early Oligocene a small sized Rhinocerotidae like Ronzotherium appeared for the first time in Europe followed by medium to large size rhinos then evolved in the upper Oligocene (Prothero et. al., 1989).

During the Miocene they showed greater diversity and well represented by six lineages that correspond to the sub-families (Aceratheriinae, Dicerorhininae, Brachypotheriinae, Chilotheriinae Iranotheriinae and Dicerotiinae) (Geurin, 2003). These lineages at least contain seven genera and thirteen species Namely, *Brachypotherium* (consisting of three species, *B. snowi, B.heinzelini and B.lewisi*), *aceratherium* (consisting of one species, *A.acutirostratum*), *Dicerorhinus* (consisting of three species, *D.leakeyi, D.primaevus, D.africanum), Chilotheridium* (consisting one specie, *C.pattersoni*), *Paradiceros* (one species, *P.mukirii*), *Diceros* (consisting of one species, *D.bicornis*) and *Ceratotherium* (consisting of two species, *C.germanoafricanum and C.simum simum*) (Hooijer, 2013).

The genus *Brachypotherium* Roger, 1904 evolved from the *Aceratheres* of the Europe which migrated to Africa as a result of exchange of elements with Eurasia during the late Oligocene. (Hooijer, D. 1978) and consists of three Miocene species, *B. snowi, B. heinzelini*, and *B. lewisi* (Cerdeño, E. 1998).

Brachypotherium snowi of Moghara is the earliest brachyophere. *Brachypotherium heinzelini* a more advanced African species found from an early Miocene site in Congo, Kenya Uganda, and South Africa and existed for 4 million years. *Brachypotherium lewisi* the last African lineage of *Brachypotherium* (Hooijer, D. 1978).

Genus *Aceratherium* of the Moghara is the earliest representative of the *Aceratherium acutirostratum* a widely distributed species in east Africa during the early Miocene. Very similar with *Dicerorhinus leakeyi* and even hard to distinguish between them when they co-occur at the same place (Hooijer, D. 1978 and 2013). *Aceratherium* consisting of the early Miocene *A. campbelli* and the middle Miocene *A. acutirrostratum*, are the first African taxa of the Eurasian origin (Cerdeño, 1998).

The Miocene African species of Genus Dicerorhinus bear a mix character of different European species and includes the species *D.leakeyi, D.primaevus,* and *D.africanum* (Hooijer, D. 1978 & 2013). The African type was characterized by the presence of two horns, somewhat constricted protocones on the upper teeth, the third molar's basal metacone bulge gives it a trapezoidal shape and smaller maxillary incisors between the lower tusks (Hooijer, D. 1978).

Genus *Chilotheridium* lived from the early Miocene to late Miocene (~10 m.y.) and with characteristic feature of tiny horned nasals, hypsodont teeth with sharply constricted protocones and antecrochets curving inward (Hooijer, D. 1978).

Genus *Paradiceros* is a *Diceros* group though it was earlier than both *Dicerose* and *Ceratotherium* with smaller two horned browsing type with reduced mandibular symphysis and lived only in Kenya (Hooijer, D. 1978).

Ceratotherium praecox, the likely ancestor of *Ceratotherium simum,* is the earliest form of the genus *Ceratotherium* (the white African rhino) and the evolution of which took place 4 to 3 mya whereas *Diceros bicornis* 4 mya (Hooijer, 2013).

Diceros bicornis, modern African black rhino which appeared about 4 million years ago in West and East Africa and some fossil specimens of the species were found in Saragata Deare in the western Afar, Ethiopia and other east African sites. A molar crown collected from Shungura formation of Ethiopia from member D (2.5 Ma) shows similar size with the modern *D.bicornis* and skull from member C (3 Ma) has already the modern characteristics. (Hooijer, D. 1978).

In particular, the longer head, enlarged lips, absence of incisor and canine teeth in both jaws, and high-crowned premolars and molars with twisted enamel aye on their biting surfaces are adaptations to grinding up gritty material in white rhinos whereas possessing the prehensile upper lip is an additional feature used to grab and pull browse in to the mouth is an adaption for browsing in black rhinos (Kingdon, 2013).

The African Miocene rhinocerotids which was independently evolved from the rest of the old world is revealed by the presence of more than one species in most genera that are different from the Eurasian similar genera and some lineages are even genetically different and peculiar to Africa. The genera *Paradiceros*, *Diceros* and certainly *Ceratotherium* are also originated in Africa.

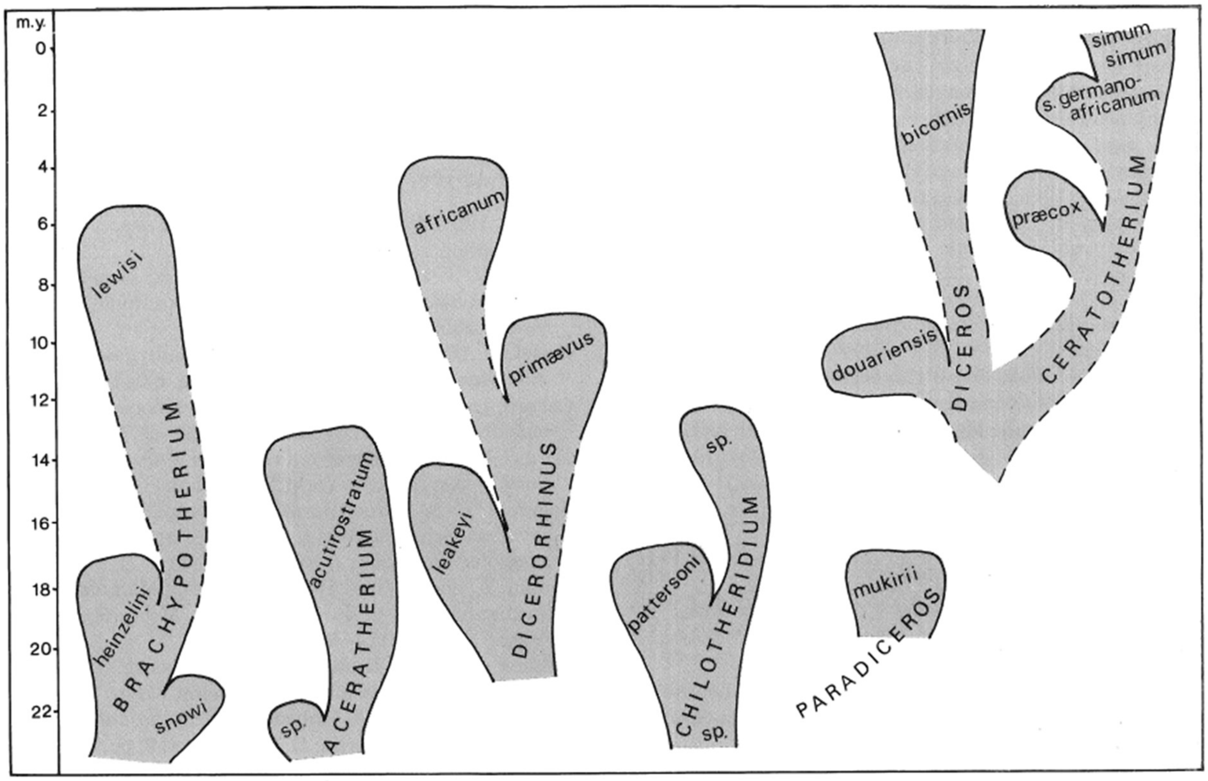


Figure 2. Proposed relationships among the fossil and recent species of African rhinoceroses, (Hoijer, 1968).

The North American Miocene rhinos are generally included into two genera, the grazer *Teleoceras* and the browser *Aphelops* or some other aceratheriine, browser-grazer pair that have been observed in their evolutionary history, particularly in savannah/woodland environments similar to the living rhinos inhibiting the East and South African savannah habitats (Prothero et. al., 1989).

Messinian salinity event, the cyclic desiccation of Mediterranean Sea in the Mediterranean and related global climatic change that occurred at the end of Miocene, caused an intense devastation and extinction on the global diversity of the animal kingdom (Prothero et. al., 1989). As a result, when the North American rhinos extinct at late Miocene, the Europe and North Asian only rhinocerotines and dicerorhinines survived in Eurasia and only dicerotines survived in Africa (Kingdon, 2013 and Prothero et. al., 1989).

There were two lineages of rhinos known from the Plio-Pleistocene of Europe and northern Asia, Dicerorhinus and Coelodonta, a lineage containing the genus of the extant Sumatran rhino (*Dicerorhinus sumatrensis*) and the second lineage is Elasmotherium whereas in Southeast Asia the one horned genus rhinoceros, a lineage of the two living Asian rhinos (*Rinoceros unicornis and Rinoceros sondaicus)* and the second lineage, Dicerorhinus were known but at the end of Pleistocene the Dicerorhinus and elasmothere lineages were extinct (Prothero et. al., 1989).

African Plio-Pleistocene is comprised of a unique collection rhinocerotids including *dicerotine,* exclusively an African tribe represented by two extant African rhinos*, Diceros bicornis and Ceratotherium simum* and other exotic lineages (Prothero et. al., 1989). *Ceratotherium*, grazer and *Dicerose*, browser is evolved from the late Miocene species *Ceratotherium neumayri,* probably a mixed feeder and the likely ancestor of both of them, as both morphologically and ecologically intermediate between the two lineages (Geraads,2005).

The modern species of *Dicerose*, *D.bicornis* originated from African *Paradicerose* during the Pliocene (4 Ma). It is the most stable and long-lived species of Africa. With the exception of northern Africa, it spread all over sub-Saharan Africa whereas, *Ceratotherium simum* evolved from *Ceratotherium praecox* (immediate ancestor to *ceratotherium simum*) between 4 and 3 Ma (Hooijer, 2013).

There are four genera and five species of extant Rhinocerotidae which are still living today, that are geographically divided into two groups: Africa and south-east Asia. *Rhinoceros unicornis* and *Rhinoceros sondaicus* are the two species of the genus rhinoceros. The species *Dicerorhinus sumatrensis* of the genus *Dicerorhinus* are the Asian group whereas *Diceros bicornis* and *Ceratotherium simum* are species of the genus *Diceros* and genus *Ceratotherium* respectively are the African group (Loose, 1975).

Rhinos were once observed in a wide range of environments except deep forests. Although they are solitary, *Ceratotherium* occasionally live in groups, which is far less common in *Diceros*. They are sedentary and territorial, consume a wide range of plant species but change their preferences based on the existing conditions. They have few natural enemies, and rarely attacked by predators (Kingdon, 2013).

They were one of the most successful group of mammals since the middle Eocene of northern hemisphere and the early Miocene of Africa despite they are at the brink of extinction today (Prothero et. al., 1986). For instance, starting from the Oligocene, they were a common component of the terrestrial habitat of the northern hemisphere and were able to cope up with most crises like environmental change, competition, migration and so on though they may not make it through their most recent crises they encounter with humans (Prothero et. al., 1989).

They adapted a wide varieties of mode of lifestyles, from cursorial, short limbed hippo like, dwarf to tapir like rhinos and combination of horns including paired nasal horns like *Diceratherium*, tandom nasal and frontal horns like Diceros , single nasal horn Teleoceras and single giant frontal horn *Elasmotherium*, (Prothero et. al., 1986).

Though they have these fascinating features, and their fossil specimens are well represented in most deposits, they are not well studied probably their large size skeletal remains make them too hard to handle them easily like other small mammals which could be the reason not to be the choice of the researchers to study them (Prothero et. al., 1986).

The general features of the two rhino lineages that lived in the Pliocene Hadar Formation and whose dietary adaptation is analyzed in this thesis, *Ceratotherium* and *Dicerose* are explained in detail below.

2.2. *Ceratotherium and Diceros*

2.2.1. Ceratotherium

Systematic Paleontology
Order: Perissodactyla Owen 1848
Family: Rhinocerotidae Gray, 1821
Subfamily: Rhinocerotinae Gray, 1821
Tribe: Dicerotini Ringström, 1924, emend.
Genus: *Ceratotherium* Gray, 1868

Ceratotherium, the genus of a square shape mouthed with broad lips that are adapted to pull the grasses out, African white rhinoceros is a pure grazer and inhibit the Great Plains of dry Africa where there is enough grassing (Owen-Smith, 1988 & Roosevelt & Heller, 1914). Morphological features like the wide mouth lacking incisor and canine high crown premolars and molars and highly folded enamel layers facilitate to adapt for grinding of abrasive diets so that to possess grazing feeding habit. (Kingdon, 2014 & Owen smith, 1988).

Evidence from the Pliocene Langebaanweg, South Africa suggested that *Ceratotherium mauritanicum* is the earliest African representative that lived until late Pleistocene and later evolved in to *C. simum* in East Africa (Geraads, 2005). The lineage first appeared some 7 mya in the form of *C. praecox* and the modern representative, *Ceratotherium simum* evolved in East Africa between 3-4 mya. (Owen smith, 1988). The fossil rhinocerotids that are represented by two genera in the Hadar Formation and constitute only 3 % of the total faunal collection and *Ceratotherium* is relatively the dominant on in any of the sub members (Campisano, 2007).

There are two sub species of the living African white rhinoceroses identified as the Southern *Ceratotherium simum simum* that inhibit from drier forms of savanna woodland with annual rainfall below 750 mm, partial to broad grassy valleys within the savanna woodland to grasslands where acacia is the dominant species and also in broad leafed savanna regions in South Africa while the Northern extinct *Ceratotherium simum cottoni* on the other hand inhibited open savanna lands where there was scattered Combretum and tall grasses during the wet season, areas like bushy/savanna or Terminalia woodland of Central African Republic, Chad, Sudan, Uganda and NE DR Congo where the annual rainfall is 1627mm (Kingdon, 2014).

The habitat preference of white rhino include semi-arid to moderately granite covered plains Combretum woodlands, mostly the woody vegetation that contain moderate to dense grass cover with dominant palatable grass species because they provide sufficient shade for them to rest in. However, they don't fond of areas of open plains with sparse tree cover and very dense low shrub strata (Pienaar, 1994). The dental mesowear analysis of this study also showed that *Ceratotherium* is a grazer.

They are selective grazers even in the presence of browse diet no white rhino was identified browsing such plants (Pienaar, 1994) but they occasionally consume woody stems but no browsers are identified so far (Kingdon, 2014). They favor short grass species included *Panicum coloratum*, *Urochloa mosambicensis*, *Digitaria* spp and *Sporobolus* spp. Early in the dry season, when they tended to stay greener than other grasses, shade grasses in particular, *Panicum maximum*, were particularly sought for (Owen-Smith, 1988). During the wet season species of short grasses like *Panicum*, *Urochloa*, *Digitaria*, *Sporobolus* and *Cynodon* constitute 50% their diet where as in the dry season they shift to graze grasses like *Panicum maximum* and *Themeda triandra* that grow under tree canopies and open areas respectively (Kingdon, 2014).

Themeda triandra is their choice of food and constitute the highest percentage of annual food intake, aromatic grasses like *Cymbopogon* spp, wirey grasses like *Aristida* spp low growing *Tragus berterionanus* are however excluded from their diet and feed on Forbs only accidentally but covers only 1% of the annual intake. (Owen-Smith, 1988). When their favorite grasses are very scarce they tend to feed on tall grasses grown on hillsides. Others like the Northern inhabitants also feed on medium-tall grasses of the genera *Hyparrhenia*, *Panicum*, *Chloris*, *Heteropooon* and *Brachiaria* but during the wet season *Brachiaria*, *Pennisetum*, Sporobolus, *Cynodon*, some forbs and *Eleusine* are their primary choices (Kingdon, 2014). Stable carbon isotope data from faeces collected over a variety of spatial and temporal scales from the semi-arid savanna of the Kruger National Park, South Africa, to test dietary predictions for African ungulates along the browser/grazer (or C3/C4) continuum indicate that C. simum shows 90% C4 grass (Codron et. al., 2007).

They are dependent on water. During the wet season they drink once or twice per day whereas during dry season when water is scarce they travel long distance in search of water left over in waterholes. It is not only for drinking but also for wallowing that hey live close to water sources. By wallowing on waterholes or muddy hallows they can remove ticks and other insects that stick themselves on their body (Pienaar, 1994).

2.2.2. Diceros

Systematic Paleontology
Order: Perissodactyla Owen, 1848
Family: Rhinocerotidae Owen, 1845
Genus: Diceros Gray, 1821

The lineage of the hook lipped African black rhinoceros (Roosevelt & Heller, 1914). The earliest representatives of the lineage first appeared in the late Miocene of North Africa and neighboring regions of the Mediterranean Sea (Owen-Smith, 1988). *Diceros praecox* is the fossil representative of this genus in East Africa that survived from the early to late Pliocene whereas *Diceros bicornis* is the living representative that evolved around 4mya and attained the present dental morphological features 2.5 mya (Owen-Smith, 1988 & Geraads, 2005).

Diceros is a browser (Fortelius & Solounias, 2000, Tylor et.al., 2013, 2014, Roosevelt & Heller, 1914) that preferably feeds on the shoot tips, stems and leaves of Woody plants, dwarf shrubs, succulent plants and herbs (Goddard, 1970),). The finger like projection prehensile upper lip that is used to grab and pull browse into the mouth, of the absence of incisor and canine teeth both in the upper and lower jaws and low crowned molars with high cusps and highly folded enamel facilitate an adaptations for browsing. (Kingdon, 2014, Owen-Smith, 1988).

Previous studies have revealed that *Diceros* can live in wide varieties of habitats including plain desert, high rain forests, and high mountainous ranges though over 91% of the living species inhibit the mountainous transition belt as these places are rich in water resources and suitable vegetation like Acacia, herbs and shrubs that serve as food sources as well as cover , shrub savanna (open plain with scattered tree) and trees and thorn shrubs savanna which have denser vegetations (Joubert & Eloff, 1971). Similarly the dental mesowear anlysis of this study show that *Diceros* is a browser.

Diceros can survive in a varieties of habitats as long as there is sufficient amounts of food enough to support the population including deserts, semi-deserts, wooded savannas, woodlands, forests and sub-alpine heartlands with annual rainfall of 100 mm to 1 300 mm. (Kingdon, 2014), including the drier savanna and arid shrub steppe from the south-western Cape to Somaliland and the northern Cameroons-Ivory Coast border with the exception of the equatorial forest region of central Africa (Owen-Smith, 1988).

They feed on low growing plants like forbs and short woody scrubs and even in open grassland grass occupies 1-5% of the feeding time whereas in semi-arid grassland plains Forbs and dwarf shrubs especially legumes such as Indigo/era, *Tephrosia, Trifolium, Lathyrus, Aeschynomene,* and *Caesalpinia* are their primary sources of food. Woody plants are also important source of food where there are insufficient growth of herbs (Owen-Smith, 1988).

Acacia, Combretum, Croton, Dichrostachys, Grewia and *Terminalia* are their primary food sources, eat Colophospermum mopane but it constitute small portion of their diet, woody plants like Boscia, Commiphora and Dobera are rejected and succulents like Euphorbia can serve as food source in the dry season (Owen-Smith, 1988).

Geographically the extinct sub species *Diceros bicornis longipes* (Western Black Rhino) lived in the savanna, Central West Africa. Another subspecies *Diceros bicornis michaeli* (Eastern Black Rhino) once lived in East Africa, Sudan, Ethiopia, Somalia to Kenya, Tanzania and Rwanda but studies revealed that today found only in Kenya Tanzania Rwanda and South Africa and the other subspecies *Diceros bicornis monor* is currently living in KwaZulu- Natal in South Africa through Swaziland, Zimbabwe, N Botswana (reintroduced), and Malawi into Western and Southern Tanzania (Kingdon, 2014).

As it is stated in Chapter Two rhinocerotids constitute only 3% of the total fossil assemblages and 1-4% of the sub-member's assemblages in the Hadar Formation. The rhinocerotids are represented by only two lineages, *Diceros* and *Ceratotherium* in which *Ceratotherium* is more dominant than *Diceros* in any of the sub-member in the Formation (Campisano, 2007).

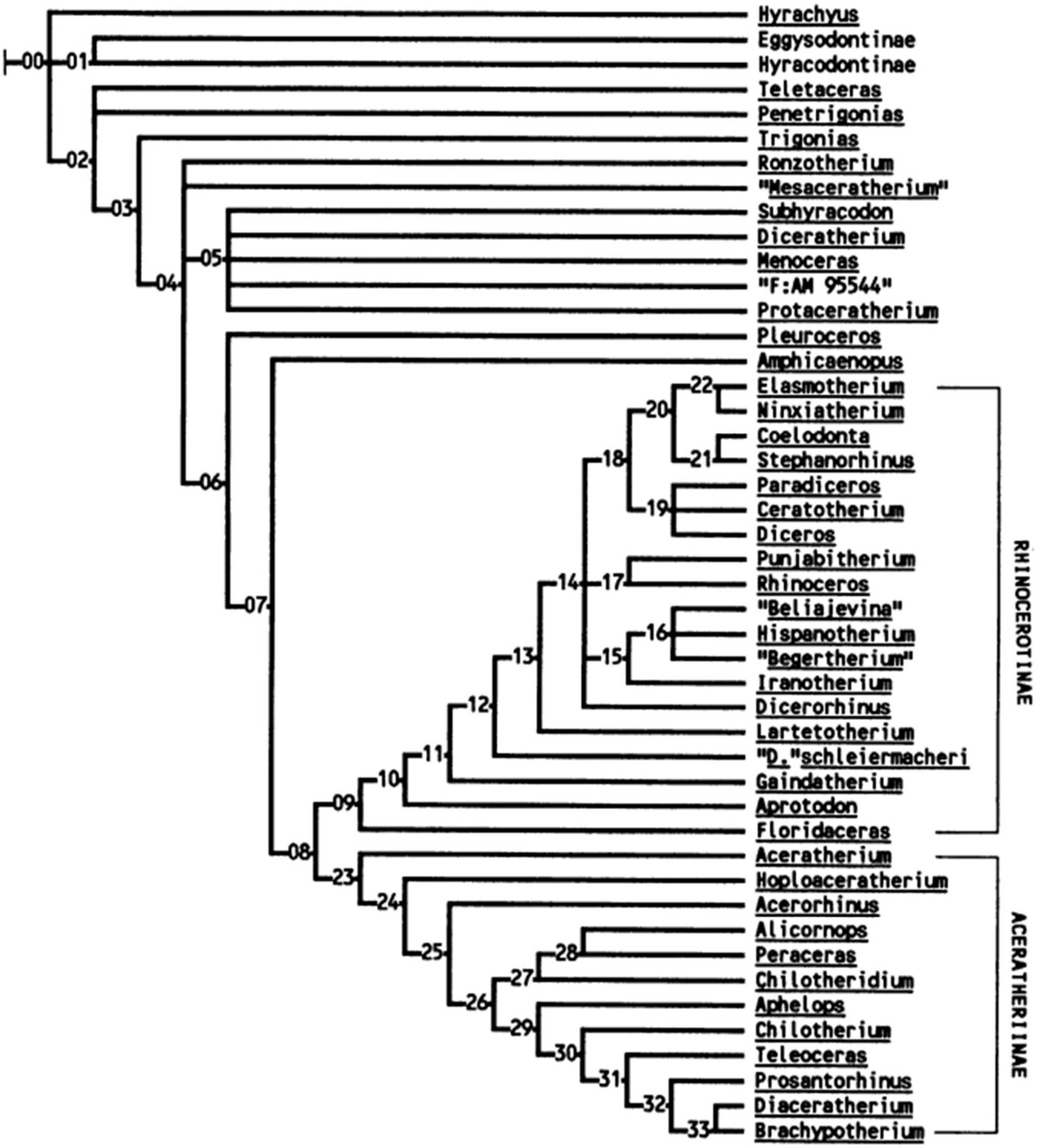


Figure 3. Cladograms for the family Rhinocerotidae, with Hyrachyus and the hyracodontid subfamilies Eggysodontinae and Hyracodontinae as outgroups, (Cerdeño, E. 1995).

2.3. DENTAL EVIDENCE OF DIATERY ADAPTATION

Information about the paleoenvironment in which the early hominids lived is important to understand their adaptation (Gray, B. T., 1980). Fossil herbivore teeth is usually used in reconstructing the paleodiet of extinct species (Fortelius & Solounias, 2000) because studying their paleodiets can provide important evidence about past ecology (Negash, 2000).

According to Mikael Fortelius, 1985 there are three main reasons that make mammalian teeth remarkably best tool in studying the interaction between growth, function, and evolution. First of all, It is able to analyze both the structure and the cell movement patterns that underpin it since the enamel's structure also acts as a record of its evolution. Changes in these patterns may be observed via phylogeny. There aren't many tissues that show how clearly ontogenetic processes are developing through morphological change. Secondly, the primary morphological categories are associated with the primary food groupings because tooth shape and function are closely correlated. This parallel development, which commonly happened to some extent, reveals dietary histories. Finally, the secondary wear-induced dental morphology offers unmistakable proof of the actual meal ingested. Fossil teeth are the best skeletal structure that might be utilized as the main source of knowledge to study the evolution of mammals since they are readily available.

According to Damuth & Janis, 2011, there are large number of extinct and extant herbivores which have high crown teeth (hypsodont). For example, living grazing ungulates have high crown teeth. Therefore, it has typically been assumed that extinct hypsodont forms were also grazers. Hypsodonty is a derived character that has been serving as a proxy to reconstruct past ecology and it has played a significant role in the evolutionary analysis of the spread of grasslands in the middle Cenozoic.

According to Lucas et.al, 2008, the structure of enamel could be especially useful as a dietary indicator for extinct taxa. The enormous features observed in the enamel cap like size, form, structure, and characteristics that covers mammalian teeth are subjects of great evolutionary interest. These traits are strongly governed by genetics and appear to be adaptive to selective pressure and contain a clear adaptive signal with regard to diet. For instance, in mammals that consume large, hard particles, thick enamel is preferred to prolong the life of teeth by providing resistance to shatter from radial fissures that occur at the enamel-dentine junction underneath. The authors also suggested that life-threatening damage in enamel originates and propagates not only from the top, near-contact surface, but also from the lower surface at the enamel-dentine. Currently there is no any theory that may describe how such variations would be appropriate enough to break food particles except some principles from other disciplines like engineering materials science, principles of fracture and deformation of solids to provide a quantitative account of how mammalian enamel may be adapted to diet. Therefore, animals that eat hard particles like seeds and dry fruits their exterior coverings appear to have evolved structures with qualities resembling enamel. Some animals like primates rely substantially on these foods in their diets, and they have been strongly linked to their evolutionary history.

The teeth of mammals that consume small, hard items or whose teeth come into contact with a lot of grit and/or phytoliths are shielded from excessive wear at the cap surface by thick enamel. We also contend that one of the cingulum's roles is to shield the tooth's neck from harm caused while chewing soft foods. Last but not least, the strong structural similarities between tooth enamel and seed casings imply that each of these materials have independently evolved a comparable defense mechanism.

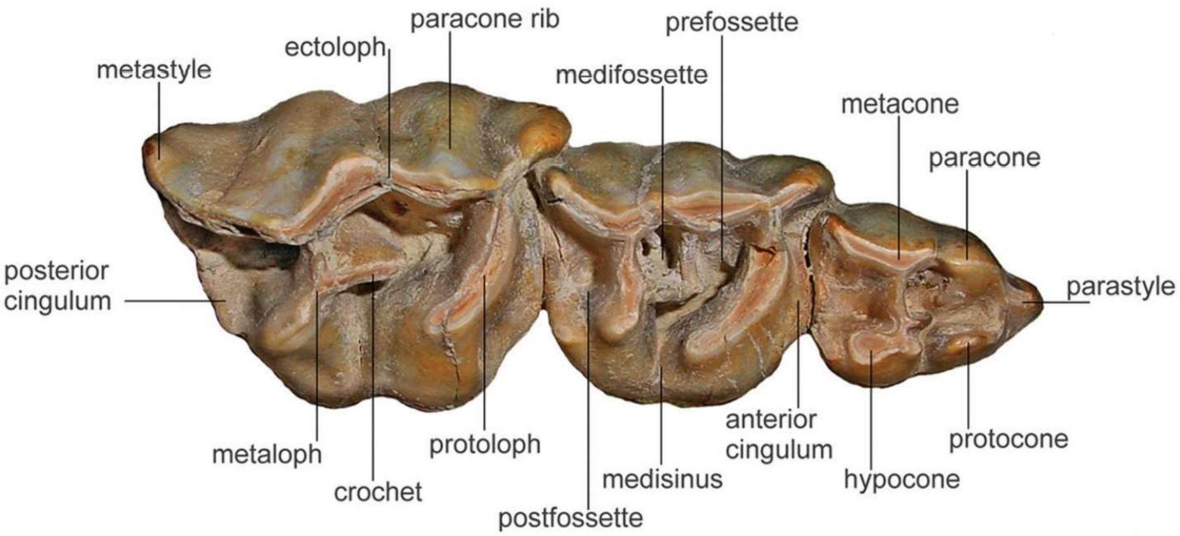


Figure 4. Nomenclature of the rhino maxillary teeth (Tong & Wang, 2014).

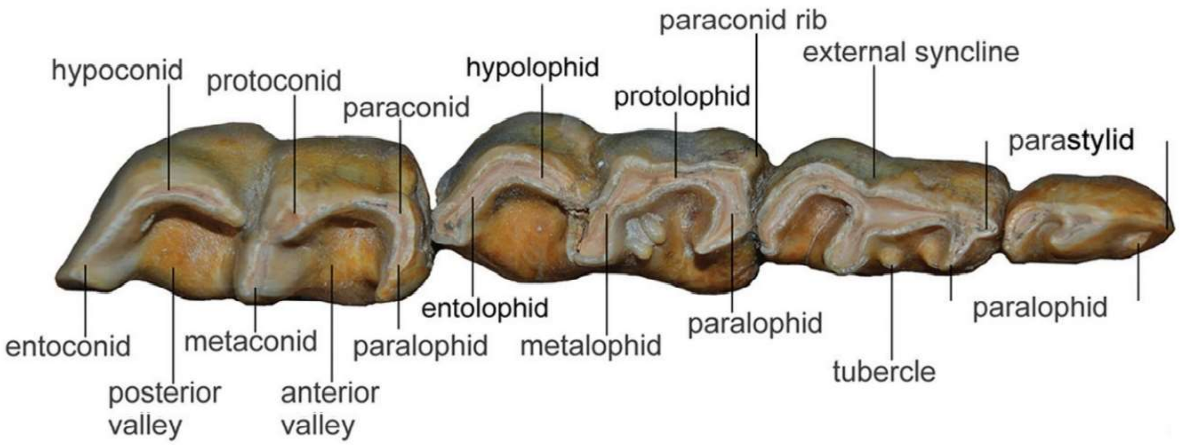


Figure 5. Nomenclature of the rhino mandibular teeth (Tong & Wang, 2014).

2.4. FOSSIL FAUNAL ASSEMBLAGE

Hadar research area is one of richest place in Ethiopia in terms of fossil remains both in variation and abundance. According to (Campisano, 2007), there are 942 localities, and 8,130 individual fossil specimens collected from Hadar and 75% of these fossil specimens were collected during the 1970s expeditions. By taking some conditions in to consideration like excluding those specimens that are not identified at least at family level; fish, birds, invertebrates, fossil woods and localities not clearly assigned in a specific stratigraphic position or with no fossils specimens, (Campisano, 2007), reduced the localities into 584, the individual specimens into 3,686 and reconstructed the analytical database of Hadar. Bovids constitute 40% the total collection, the most abundant of all fossil specimens in Hadar and then Suids (14%) followed by elephantids (9%).

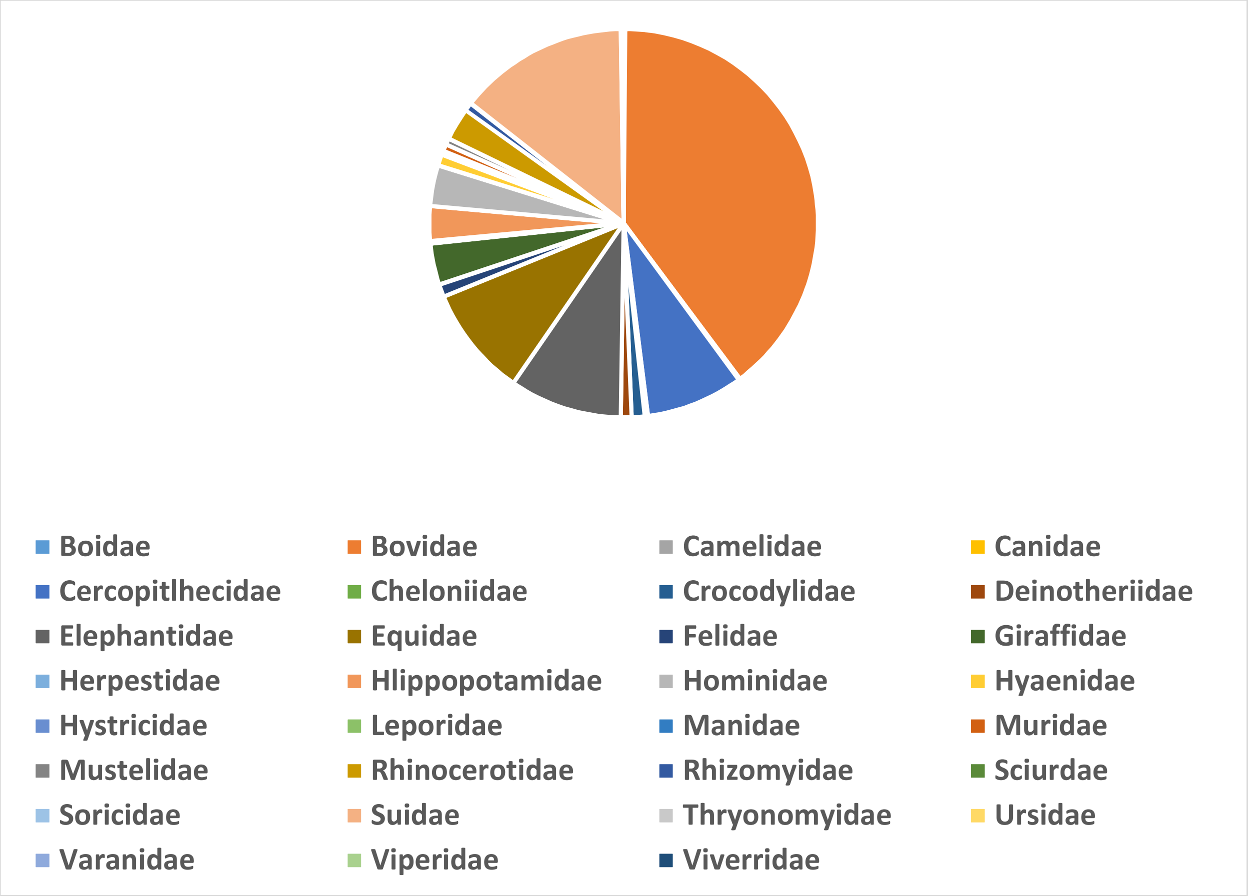


Figure 6. Number of specimens per mammalian family collected from the Hadar Formation (the raw data are taken from Campisano, 2007).

On the other hand, rhinocerotids constitute 3% of the total fossil assemblage and 1-4 % of a submember's assemblage of the Hadar *Ceratotherium mauritanicum* and *Diceros praecox* are the only rhinocerotids species identified in Hadar, but most of the rhinocerotids fossil specimens are not identified and categorized under specific genus. Generally, genus *Ceratotherium* is more dominant than genus *Diceros* in any sub-member (Campisano, 2007).

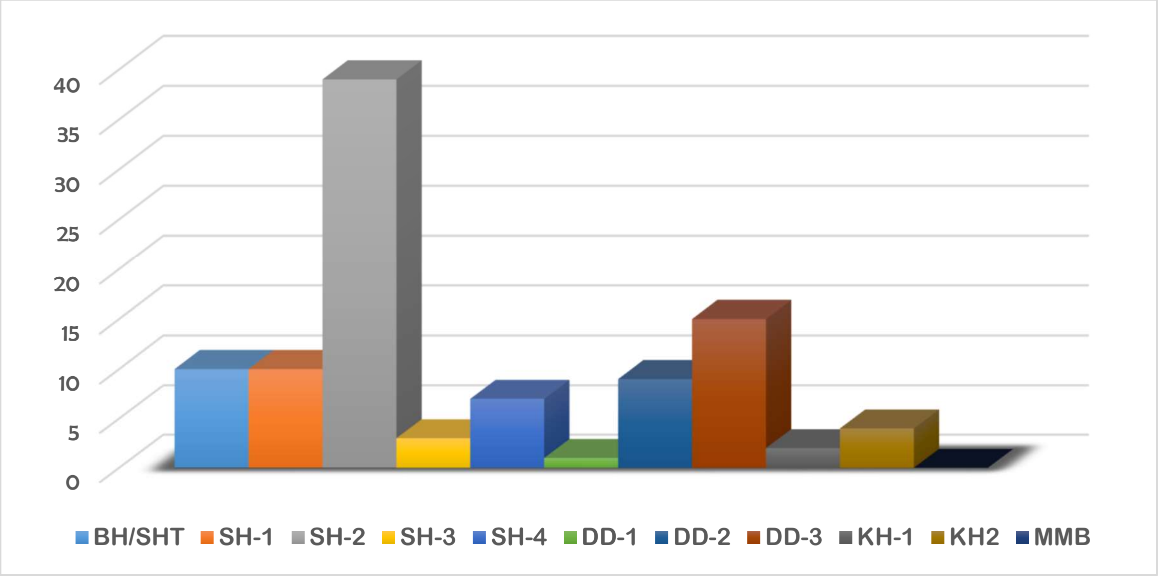


Figure 7. Rhinocerotidae as a percentage of all Hadar mammals per sub member. (The raw data are taken from Campisano, 200)

2.5. PALEOECOLOGY HADAR FORMATION

The fossiliferous hominin bearing Hadar Formation consists of a mosaic of habitats that existed at different time periods with varying proportion resulted from changes in the local climatic conditions but generally intermediate cover habitats of bushland, open woodland, and shrubland with varying regions of wetlands or edaphic grasslands were the prominent habitats through time (Kaye reed 2008 & Johanson et.al. 1982).

Sidi Hakoma Member is located above the Basal Member and include sediments deposited between the base of the Sidi Hakoma Tuff (SHF) and the base of Triple-Tuff (TT-4) and consists of four sub members namely SH-1, SH-2, SH-3 and SH-4 that span between 3.42 & 3.26Ma where SH-1 & SH-2 spans between 3.42 to 3.35 and SH-3 & SH-4 spans between 3.35 to 3.26Ma. (Campisano and Feibel, 2008). Depositional condition of the lower Sidi Hakoma member (SH-1 & SH-2) is fluvial conglomerates and sands interbedded with laminated siltstones and vertic paleosols, SH-3 Dark gray to green laminated mudstone and local limestones rich in remains of fish and gastropods and single dark brown vertisol close to the top of the member (Quade et. al. 2004).

There was high annual rainfall and less seasonal environment with only three months of dry season detected from the mammalian adaptation and oxygen and carbon isotope analyses of mollusks (Kaye reed, 2008). 800-1200 mm/year of precipitation and 15.5°C to 24.8°C of temperature values are recorded throughout the whole sequence but the highest value of precipitation with an increased humidity was recorded between 3.37 and 3.35 Ma. (Bonnefille et. al, 2004).

The palynological analysis by (Bonnefille et. al., 2004), showed that Typha that grow on the flat and soft soil near to the river bank or lakes, Cyperaceae (sedge), and Gramineae (grasses) are the dominant spp. suggesting a wide spread cover of herbaceous plants around the paleolakes, the presence of aquatic Laurembergia and high Cyperaceae typical of the present highland swamps, varying amount sedges on the other hand is indicative of fluctuation of the water level in Hadar.

Based on (Campisano, 2007), the fluvial BM/SHT can be characterized as a mosaic of woodland and bushland revealed from the faunal assemblages. The high proportion of Notochoerus followed by Nyanzachoerus indicative of relatively closed habitat like wooded savanna or forest fringes. High proportion bovids like bovines represented by Ugandax suggestive of closed habitat and aepycerotines but low proportion of reduncines is recorded in BM/SHT. The low abundance of cercopithecids indication of the absence of thick gallery forest. The proportion of suids is lower than the lower members whereas hominins and cercopithecids showed their highest abundance compared to of the whole sequence of Hadar Formation and the faunal assemblage during SH1 time shows a simultaneous decline in Eurygnathohippus proportions and an increase in the diversity and proportion of closed habitat folivores, including some primates, cephalophines, neotragines and giraffids.

The Basal and lower Sidi Hakoma Members consists of mammals like Aepyceros, Ugandax, and Potamochoerus that are dominant in a series of marshy lake edge environment that are interrupted by distributary facies that contain suids like Notochoerus and Nyanzachoerus, bovids like Tragelaphus and abundant elepantids, indication of bushy to forest habitats with bhigh water availability (Gray, 1980). Johanson et.al. 1982, added that Basal Member and SH-1 to SH-3 the lake was limited size and surrounded by marshy areas.

The pollen fossil records of the Hadar Formation indicate the lower member consists of evidences of deciduous and evergreen/bushland later replaced by high altitude humid forest taxa where as in the upper Sidi Hakoma and Denen Dora succession from woodland to wet and dry grassland but at 2.95Ma conifer forest, Juniperus abundantly recorded though existed through the whole sequences of the Formation but arboreal taxa of the arid steppe like Commiphora, Acacia, Grewia, Capparidaceae, and riverine forest like Combretaceae and Tamarix were very scarce (Bonnefille et. al, 2004).

According to (Bonnefille's, 1987) palynological study of Hadar that covers the age ranging between 400,000 and 3.3 Ma, SHT is characterized by its floral diversity. Gramineae, Cyperaceae and Typha, Typha were present in H-2 indication of fresh water and Marshes were also developed on flat areas around the shallow lakes. Presence of aquatic plants like Polygonum indication of fresh water swamps. Ever green bushlands and montane forests were also present but in lower distribution than SHT spectrum. In the upper pollen zone (H-3) taxa including Ilex, Myrica and Hagenia associated with arboreal taxa like Prunus africana, Olea and Juniperus as well as elements of the montane forests with Hagenia abyssinica, Ilex and Prunus but few taxa of evergreen bushland are recorded. The spectra found near the gastropod beds (pollen zone H-4) contain large taxa of grasses but taxa like Cyperaceae , Typha, and montane forest are low in this spectrum indicative of the extension of the grass land vegetation by replacing evergreen bushland, swamps and marshes.

In general based on the analyses of fossil pollen recovered from the Hadar Formation indicate a forested habitat in the Sidi Hakoma Member. Denen Dora Member reflects a drier habitat and Kada Hadar Member was more wooded and humid (Bonnefille et. al, 2004).

According to (Bonnefille, 1987), the present vegetation of Hadar is classified as subdesert steppe or Acacia-Cornrniphora grassland and shrubland that are similar to the semi-desert vegetation found in the southern Afar depression and located at the arid regions of mean annual precipitation less than 400mm, mean annual temperature of 29°C and 3600 mm/year of evaporation. The dominant tree types of the region include Balanites aegyptiaca, associated shrubs like Cadaba rotundifolia and Grewia tenax. Along the temporary water courses trees like Salvadora persica and Ziziphus mauritiana are grown whereas permanent riparian vegetation are developed along the Awash river specially in the meanders while Acacia woodland is frequent along the basaltic plateau and rocks slopes of the escarpment and the presence of Pediastrum algae Diatom, diatom Melosira granulate Ostracod indication of lacustrine conditions.

There are four biomes identified in Hadar, steppe (STEP) Tropical Xerophytic Woods/Scrub (TXWS) Temperate Xerophytic Woods/ Scrub (XERO) and Broad-leaved evergreen/Warm Mixed Forest (WAMF). While the first three biomes show permanent appearance in Hadar the last biome shows repeated appearance and disappearance at different times (Bonnefille et. al, 2004).

The biomes, plant functional types and associated major taxa are listed in table 4.

	Biome	Plant functional types (PFTs)	Major taxa
1	steppe (STEP)	steppe forb, grass	Aerva, Capparis decidua and Gramineae
2	Tropical Xerophytic Woods/Scrub (TXWS)	Tropical sclerophyll succulent and grass	Alchemilla, Cliffortia, Dendrosenecio, Ericaceae, Helichrysum*, Lobelia, Protea, Stoebe kilimandscharica and Gramineae
3	Temperate Xerophytic Woods/ Scrub (XERO),	temperate sclerophyll/succulent and grass	Amaranthaceae/Chenopodiaceae, Compositae tubuliflorae
4	Broad-leaved evergreen/Warm Mixed Forest (WAMF).	wet tropical raingreen , dry tropical raingreen	Afrocrania volkensii, Apodytes dimidiata, Hagenia abyssinica, Hypericum, Ilex mitis, Juniperus procera, Myrica, Olea, Podocarpus, Polyscias fulva*, Prunus africana, Rapanea melanophloeos, Schefflera myriantha*, Sericostachys scandens

Table 1. The major biomes in Hadar (Peyron et. al., 2000)

	Habitat condition	evidence
1	Fresh water lacustrine conditions.	The presence of fossil potamid crabs
2	Shallow lacustrine or marsh conditions, with abundant surrounding vegetation.	lignite coal deposit in Unit SH-3
3	Open woodland or well-watered highland wooded savanna conditions.	Tachyoryctes Oenomys and Mastomys, (rodents)
4	wooded savanna or open woodland conditions	Nyanzachoerus (suid), the African giant forest hog, tragelaphine (bovid) and Colobus monkeys.
5	more open habitats, wooded to treeless savanna	Giraffa, Aepyceros, alcelaphine bovids, Hipparion, Diceros and Ceratotherium
6	Easterly flowing streams from the Ethiopian plateau, 0 to 20 km to the west of Hadar, emptied into a into a shallow lake with a broad flat floodplain	indicated by finds of ostracods

Table 2. Summary of habitat conditions and their respective faunal evidences in Hadar (Boaz, 1977).

Submember	Arboreality	Terrestriality	Fruit and Leaves	Grazing	Mixed feeding
Basal	Bushland 4%	Grassland 78%	Woodland 11%	Bushland, woodland, shrubland 11%	Bushland 18.5%
SH-1	Bushland 4%	Bushland, woodland, shrubland ecotone 74%	Closed woodland 26%	Bushland, ecotone 4%	Bushland 18.5%
SH-2	Bushland, woodland 3%	Grassland 80%	Woodland 13%	Bushland, woodland, shrubland 13%	Bushland, woodland, ecotone, shrubland 13%
SH-3	Shrubland, grassland 0%	Grassland 82%	Shrubland, grassland 9%	Bushland, ecotone 9%	Bushland 18%
SH-4	Shrubland, grassland 0%	Bushland, grassland 76%	Bushland, woodland, ecotone 14%	Bushland, ecotone 5%	Bushland 19%
DD-1	Shrubland, grassland 0%	Grassland 81%	Bushland, woodland, ecotone 13%	Bushland, woodland, shrubland 13%	Bushland, woodland, ecotone, shrubland 13%
DD-2	Bushland, woodland 3%	Bushland, grassland, ecotone 75%	Shrubland, grassland 9%	Bushland,woodland, shrubland 13%	Bushland, woodland, ecotone, shrubland 16%
DD-3	Shrubland, grassland 0%	Grassland 82%	Shrubland, grassland 7%	Bushland, woodland, shrubland 14%	Grassland 21%
KH-1	Shrubland, grassland 0%	Grassland 83%	Woodland, shrubland 10%	Woodland, shrubland 17%	Grassland 21%
KH-2	Bushland, woodland 2.5%	Grassland 83%	Woodland, shrubland 10%	Woodland, shrubland 15%	Bushland 16%
MAKA	Shrubland, grassland 0%	Grassland 86%	Shrubland, grassland 7%	> Grassland 25%	Grassland 21%
DANA	Shrubland, grassland 0%	Grassland 86%	Shrubland, grassland 7%	> Grassland 32%	Bushland, woodland, ecotone, shrubland 14%

Table 3. Hadar sub-members and their habitat classifications for each of the five significantly different adaptations (Reed, 2008).

2.6. PREVIOUS WORK AT HADAR FORMATION

A number of studies have been conducted on the Hadar Formation with different proxies aimed at reconstructing mammalian Paleodiet and the paleoenviroment of the area. Paleoecological patterns including reconstructing habitats from fossils materials, identifying the temporal and special habitat and species changes, and examining variations in mammalian adaptations and species abundance related to habitat differences were carried out. By examining the different patterns in these assemblages, it is possible to identify the relationship between climate, local and regional geology, and other elements that provide contextual meanings important to understand the evolution of hominins (Reed, 2008).

Boaz, 1977, reconstructed the paleoecology of the Hadar Formation based on the types of fossil faunas and their respective diets. The findings include rodents, suggests that there were open woodland or well-watered highland wooded savanna conditions. Nyanzachoerus a Suidae having low crowned molars and that may have comparable habitat to those of extant Hylochoerus, indication of wooded savanna or open woodland. The presence of Giraffa, Aepyceros, alcelaphine bovids, Hipparion, Diceros and Ceratotherium suggest that more open habitats, wooded to treeless savanna. Generally, the Hadar localities represent paleoenvironments ranging from wooded savanna to treeless savanna.

Deciduous and evergreen forest and bushland elements can be found in the bottom part of the Sidi Hakoma Member whereas the upper portions of the Sidi Hakoma and Denen Dora Members show a succession of wet grassland, woodland, and dry grassland and a slight expansion of forest biome in youngest portions of Kada Hadar Member (Grine et. al., 2006).

According to (Reed, 2008), the paleohabitats of most of the hominin bearing Hadar Formation is varying between the intermediate cover habitats of bushland, open woodland, and shrubland with variable regions of wetlands or edaphic grasslands across time. However, there is no pattern in the transition through time from wet, closed habitats to those that are dry and open, while there can be a steady drying trend amidst variations. Between ~3.42 - ~3.45Ma (Basal Member) faunal specimens from this member includes bovids like Alecelaphins an indication of open areas, Tragilaphins and Aepycerotini indicating from a more wooded to lightly wooded lands. Between ~3.42- ~3. 26 the Sidi Hakoma Member consists of 4 subunits, SH-1, SH-2, SH3 and SH-4 There is low ratio between alecelaphins and antilopins. The analysis based on the mammalian adaption indicates that there was higher annual rainfall and less seasonal environments in SH-1. The habitats of SH-2 is similar to the habitats of Basal Member. Bovids like reduncini and hippopotamids are found in SH-3, indication of scrub woodlands and grasslands may have been associated with floodplains or wetland habitats. Analysis of SH-4 indicates that it has similar habitat to SH-3 except higher abundance of bovids (reduncini) in SH-4 an indication of transgression of Lake Margin wetlands. In the Denen Dora-1 (DD-1) section there is a slight increase in the abundance of bovid specimens when compared to SH members indicating an overall woodland habitat. Bovid (reduncini) recovered from DD-2 suggests the habitat was a wetland or floodplain habitat. There is significant increase of alcelaphins in DD-3 indicating grassland habitat whereas the decrease in the abundance of reduncini suggests dry habitat. In KH-1 the abundance Antilopins increased while Alcelaphins decreased indicating it was most likely an open woodland with some edaphic grassland habitat. The faunas in KH-2 includes Antilopini and Alcelaphini bovids, indicating dry environment and open habitat. Despite the overall change of species composition in Hadar formation at 3Ma it might indicate an ecological shift. There are species that are ecologically found in a wide range of environments and well distributed in all the sub members so habitat change, and species representation may imply the responses to local and or regional climate fluctuations and local geological events.

2.7. GEOLOGY OF THE STUDY AREA

The fossiliferous Pliocene Hadar formation is located at the lower Awash Valley of Afar depression of Ethiopian rift, Afar regional state, Ethiopia. A~155 m thick and well-preserved strata of the Hadar formation that lies 500 meters above sea level is rich in mammalian fossil specimens including hominins like the famous Australopithecus afarensis (Lucy) which can provide basic information about the early homonin evolution (Campisano and Feibel, 2008).

A number of Studies that have been undertaken for decades in understanding the paleoenviromental and stratigraphic context of vertebrate faunas revealed the large number of chronostratigraphic sequences of the Hadar and the overlying Busidima formation. The paleomagnetic age and Radiometric dates (Ar40/Ar39) show that these sequences consist of sediments that spans the intervals between ~3.8Ma and ~2.94Ma and are divided in to four members. Namely, Basal member

(BM) found at the base of the formation (3.42Ma-~2.38Ma), followed by Sidi-Hakoma(SH) member (~3.42Ma-3.24Ma) followed by Dennen Dora (DD) (~3.24Ma-3.2Ma) and then followed by the last member of the Hadar formation called the Kada-Hadar (KK) member (~3.2Ma-2.94Ma) (DiMaggio et al., 2015).

These members are further divided into sub-members based on their lithostratigraphic markers specifically sands. The sub members are SH-1, SH-2, SH-3 and SH-4 for Sidi Hakoma member; DD-1, DD-2 and DD-3 for Denen Dora member and KH-1, KH-2 and KH-3 for Kada Hadar member and some sub members are also sub divided into smaller subdivisions called units (DiMaggio et al,2015). The units are BM2s in the basal member, SH1s, SH2s and SH3s in the SidiHakoma member DD1s, DD2s and DD3s in the Denen-dora member and KH1s, KH2s, KH3s and KH4s in Kada-Hadar member (Campisano and Feibel, 2008).

Overlying at the top of the Hadar formation, the Busidima formation lies on, an angular unconformity separated by Busidima unconformity surface and it spans the period between 2.69Ma and 0.16Ma and it is home for fossil hominins like Homo habilis and Homo erectus including the earliest stone tool artefacts. (DiMaggio et al., 2015).

The depositional environment of the Hadar formation is predominantly fluviolacustrine deposits (Johanson et.al., 1982) with continuously oscillating between fluvial and lacustrine observed from the sand bodies deposited at the different stratigraphic levels by the meandering and associated fluvial systems (Campisano and Feibel, 2008) and an extensive lake that periodically fill the entire sedimentary basin (Johanson et al.,1982).

Like other African Plio-Pleistocene mammalian localities fossil representatives of the two extant rhino lineages were once lived at the Hadar Formation, Ethiopia. (Guerin, 2003 and Geraads, 2005). Genus *Ceratotherium*, represented by *Ceratotherium mauritanicum*, the first fossil rhino species ever named in Africa and genus *Dicerose*, represented by *Dicerose praecox* co-occurred in the Pliocene Hadar Formation (Geraads, 2005).

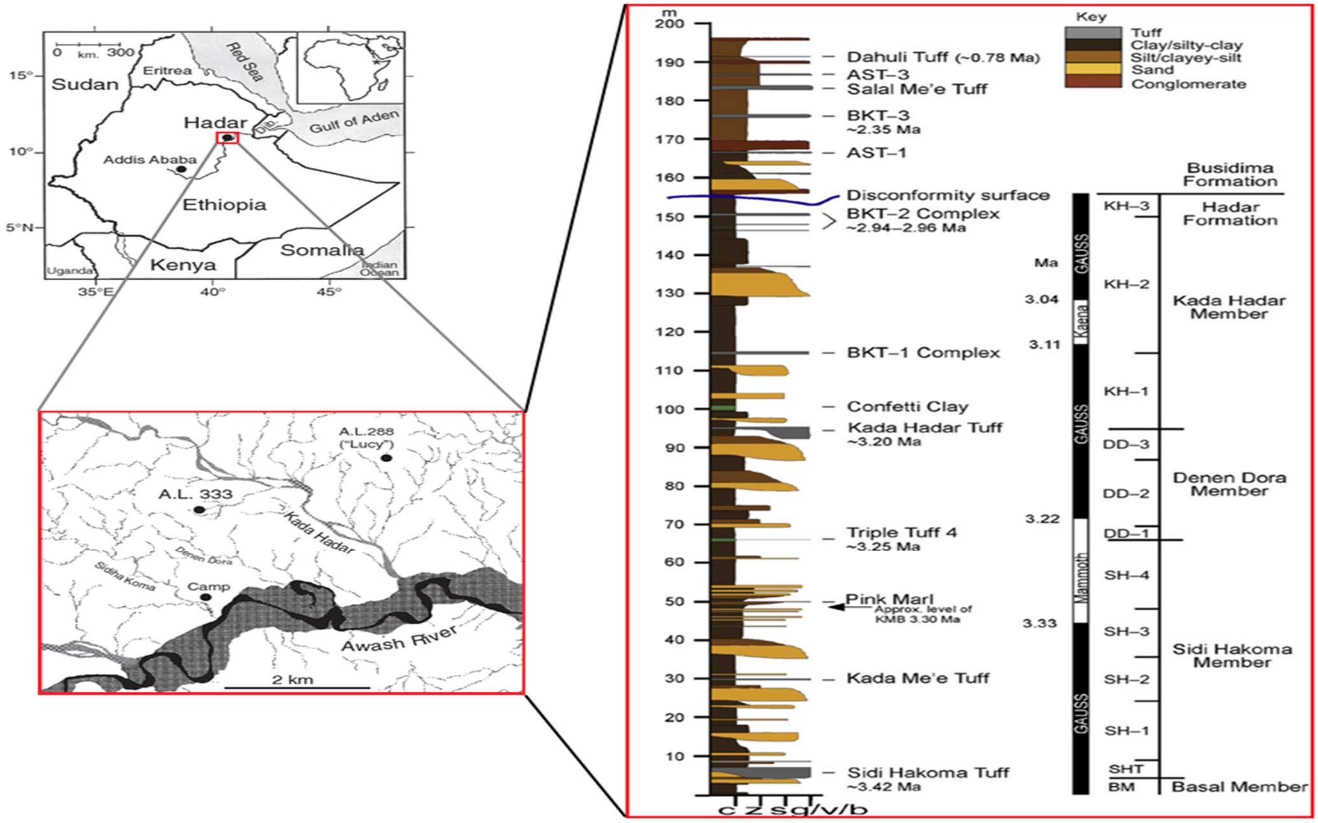


Figure 8. Hadar study area and Composite stratigraphic section of the Hadar and Busidima Formations. Tuffs and major marker beds are labeled alongside the section. Adapted from Campisano and Feibel, 2008.

CHAPTER THREE MATERIALS AND METHODS

3.1. MATERIALS

The fossil specimens for the proposed study are housed at the Ethiopian Heritage Authority, EHA in paleontology collection, Addis Ababa, Ethiopia. Almost all the necessary information like their taxonomy, stratigraphic position, localities, and so on are found well documented in the revised catalogue of 2017 by Hadar Research Project and are free to access. The samples required for dental mesowear analysis include 19 teeth samples of *Diceros praecox* 18 of which are from Sidi Hakoma member (SH-1) and one tooth from Denen Dora (DD-2) and 28 teeth samples of Ceratotherium mauritanicum, 27 of these samples are recovered from Sidi Hakoma member (SH-1) and 0ne from Kada Hadar member (KH-2). A total of 46 rhinocerotids fossil teeth collected from Hadar Formation since 1970s expeditions and well represented at Hadar Formation and the study was mainly focused on the upper cheek teeth (P2-M2). The mesowear pattern of the fossil species was investigated through comparisons with existing database of previous studies.

3.2. SAMPLE SELECTION

The fossil teeth specimens for the analysis were selected only from Sidi-Hakoma member because the other members contain very few specimens not enough to make inference, they were excluded from the analysis. According to (Fortelius & Solounias, 2000). A sample of less than ten specimens should be treated with caution, while more than 30 is probably excessive.'

Because it is difficult to find the complete skeleton and they are usually found in isolated form with few numbers, each sample represents one individual.

The maxillary second, third, fourth premolars, first and second molars of only the permanent teeth were selected and scored using single cusp scoring for the anterior and posterior cusp position separately (Tylor et. al., 2013). The first upper molar was excluded as it didn't consistently appear in both groups and the third upper molar was also excluded because as it is explained by (Tylor, 2013) it has reduced ectoloph compared to other cheek teeth.

Teeth which were in a very early and late wear stages and teeth where their cusps are either damaged or modified by structural elements were excluded in order to establish stable mesowear equilibrium (Kaiser, 2009).

3.3. METHOD

It is impossible to directly observe the biotic (plants and animals) and abiotic (rain, temperature) components of the ancient world as they all are extinct. Therefore, a different approach is necessary to understand and reconstruct their paleoecosystem based on the physical and chemical evidence they left on the geological records (D. A. Croft et al., 2018).

In this study the paleodietary adaptation and paleoecology of the family rhinocerotidae (Mammalia: Perissodactyla) collected from the Pliocene Hadar Formation was reconstructed using the adjusted mesowear method for rhinos by Taylor et. al., 2013 for the maxillary teeth. Mesowear is one of the methods used to reconstruct the diet of herbivores based on the macroscopic dental wear patterns produced over a long period of time (from months to years) (Croft et al., 2018). Therefore, it represents the typical diet of a particular species from a particular area in space and time (Fortelius and Solounias 2000).

The mesowear method analyzes the macrowear patterns of ungulate teeth (Fortelius & Solounias, 2000) based on the facets developed on the occlusal surfaces of cheek teeth which implies the relative proportions of attrition and abrasion (Winkler and Kaiser, 2011). Attrition is created when teeth move against each other (tooth-on-tooth contact), characteristic feature of herbivores that feed on leaves of dicotyledonous plants, twigs, buds, flowers, and fruits known as browsers whereas abrasion is created when teeth contact to extraneous materials which is observed in herbivores that feed on grasses and other low growing vegetations known as grazers (Croft et al., 2018). Attrition (tooth-tooth contact) creates facets whereas, abrasion (tooth-food contact) eliminates the facets (Winkler and Kaiser, 2011).

The classical mesowear method analyzed wear patterns developed on the buccal cusps of maxillary M2 to infer the general diet through observation of occlusal relief (OR) expressed as high (H) or low (L) and cusp shapes (CS) as sharp (S), round (R) or blunt (B) (Fortelius & Solounias, 2000).

Cusp shape implies the shape of the cusp tips created as a result of facet development whereas occlusal relief refers to the relative difference in height between cusp tips and inter cusp valleys as seen in buccal projection, i.e., how high the cusps appear in lateral view (Fortelius & Solounias, 2000).

The extent of facet development shows the dominancy of abrasion or attrition. In browsers attrition is dominant with high (H) occlusal relief (OR) and sharp (S) cusp whereas, in grazers abrasion is dominant with low (L) occlusal relief (OR) and blunt (B) cusp (Fortelius & Solounias, 2000).

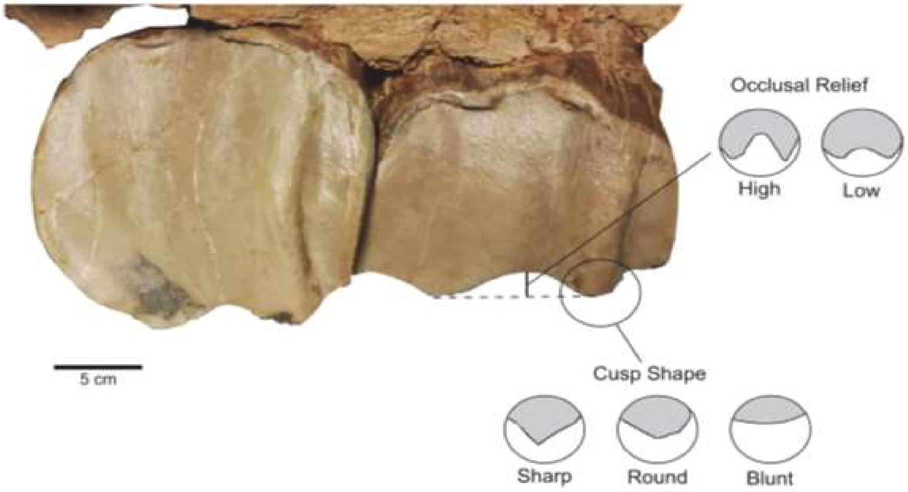


Figure 9. Principle of mesowear scoring with the main variables (Hullot et al., 2021).

It is possible to create a more distinct measure of wear by extending the mesowear categories and employing single cusp scoring method, that could enable to identify wear pattern variations within the tooth and cusp, and this resulted in new approaches on the diets, intake, and mastication of rhinos (Tylor et. al., 2013).

For instance, different inter-cusp wear pattern was observed using adjusted method which may be related to morphological adaptation to a particular diet. Especially in *Diceros bicornis* in which the anterior cusps consistently showed abrasion dominated patterns than the posterior cusps might make it easier to grind up heterogeneous browse, though it is barely observed in *Ceratotherium simum,* where there are almost uniform inter-cusp wear patterns which may facilitate to grind up physically more homogenous grass (Tylor et. al., 2013).

The classical mesowear method of (Fortelius & Solounias, 2000) includes two categories of OR that are ‘high’ (≥0.03) and ‘Low’ (< 0.03) and three categories of cusp shape, ‘sharp’ ‘round’ and ‘blunt’.

Tylor et. al., 2013 adjusted the method based on the extended mesowear method of Winkler and Kaiser, 2011 to make it suitable to work with rhinos. According to the new method two intermediate stages of occlusal reliefs are introduced. The scores are high-high (hh) for high reliefs with valley angle ≤ 90^{o} and high-low (hl) for intermediate wear stages between the high and low scores in the classical mesowear. Because the occlusal relief boundary is difficult to differentiate visually, Tylor et. al., 2013 added another category of flat negative (fn≤0) that clearly differentiate the boundary.

Two more cusp shape scores are added. These are round-harp (rh), cusps that are sharp when seen with the naked eye but sharp when seen through a hand lens. The second one is round-round (rr) The score round-round (rr) accommodates intermediate stages between the conventional scores round and blunt. Round-round classifies a not yet blunt cusp, the height of which at the highest point is half as long (or shorter) as length of the rounded cusp.

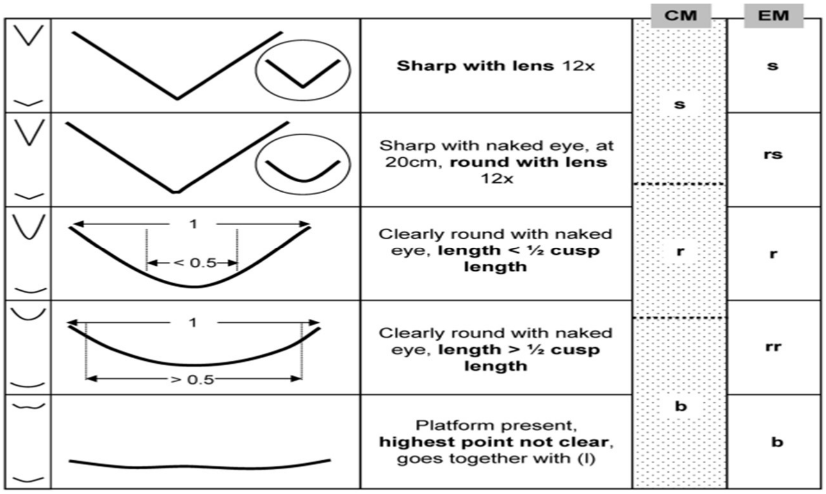


Figure 10. Cusp shape categories for the classical mesowear method of Fortelius and Solounias, 2000 ***(CM)*** *and adjusted mesowear method for rhinos of Tylor et. al., 2013* ***(EM)***

The adjusted method of Tylor et. al., 2013 includes 5 categories of cusp shapes, s = ‘sharp’, rs = ‘round-sharp’, r = ‘round’, rr = ‘round-round’ and b = ‘blunt’ and five categories of occlusal relief, : hh = ‘high-high’, h = ‘high’, hl = ‘high-low’, l = ‘low’ and fn = ‘flat-negative.

The EM(R)-S, OR and CS were each converted into a score, which ranged from 0 'high-high' up to 4 'flat-negative' (EM(R)-S) in OR, and from 0 'sharp' to 4 'blunt' in CS as follows:

Occlusal relief	High-high	High	High-low	Low	Flat negative
Mesowear score	0	1	2	3	4
Cusp shape	sharp	Round-sharp	round	Round-round	blunt
Mesowear score	0	1	2	3	4

Table 4. Combination of mesowear variables and their respective mesowear scores for the adjusted mesowear method by Tylor et. al., 2013.

Finally, each score was converted in to average and the mean score value was computed for each group and compared with the results of previous research.

According to Tylor et. al., 2013 *'The height of the cusp was taken from the apex of the cusp (anterior or posterior) down to the line connecting the inner valley and the outside edge of the tooth, and the length was taken as the total length of the tooth. Total tooth length was used, rather than cusp length, because the divide between cusps was often ambiguous, whereas total tooth length was a consistent measure*.'

Due to asymmetry of rhino teeth Occlusal Relief is difficult to determine visually. As a result, digital caliper was used to measure the anterior and posterior cusp position separately and a hand lens to determine the cusp shape when necessary (Tylor et. al., 2013).

3.4 STATISTICAL ANALYSES

The statistical analysis of *Ceratotherium* and *Diceros* were carried out first by converting the mesowear variables in to mesowear score values then calculating the cusp shape (CS), occlusal relief (OR) and mesowear score (MS) mean values. Intraspecific statistical significance test for tooth position differences in the anterior and posterior cusp positions and comparison of the two sides along the whole tooth row were conducted using One-way ANOVA test whereas cusp difference in each tooth position were conducted using two sample t-test. Statistacal data analyes and manipulation of the data were conducted by using PAST (PAleontological STatistics) and Microsoft excel. The critical significance value was $P < 0.05$.

CHAPTER FOUR RESULT

In this chapter the results of the dental mesowear scores of the fossil Diceros and Ceratotherium are presented. Data manipulations like statistical data processing, calculating and plotting were done by using statistical software called PAST (PAleontological STatistics) and Microsoft excel.

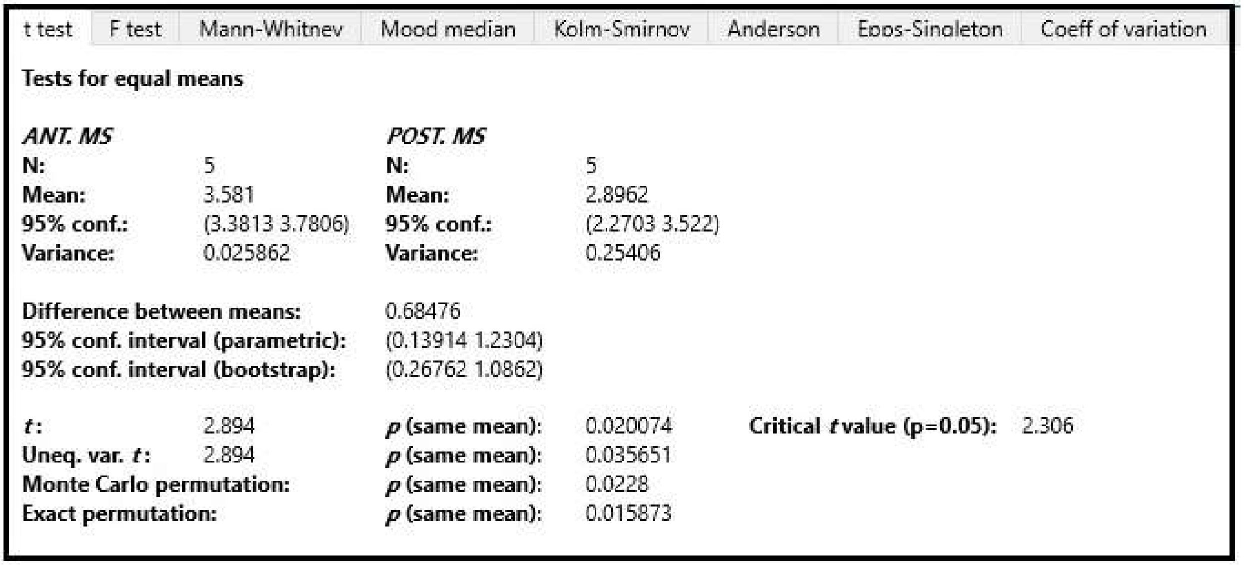
The results are presented in the form of box plot as it provides the graphical summary of the data and enables us to quickly identify the mean values and dispersion of the data set. In the box plot each box represents 50% of the data with the median value and the whiskers representing 25% of the data.

Statistical test was conducted to test if there is significant inter and intraspecific difference in the cusp and tooth positions. As a result, interspecific score differences, intraspecific cusp differences and tooth position differences were tested separately in the anterior and posterior cusp position using two sample t-test and the summary of the results are presented in table. The critical t-value was set to $p < 0.05$.

Taxa		**P2**		**P3**		**P4**		**M1**		**M2**	
		A	P	A	P	A	P	A	P	A	P
Diceros	n	3		3		4		4		5	
	CS score	3.666667	1	3.33333	1	1	0	2.5	0	2.2	0
	OR score	3.333333	2	2.666667	1	2.75	1.25	2.5	1.25	2.2	0.4
	Mesowear score	**3.5**	**1.5**	**3**	**1**	**1.875**	**0.625**	**2.5**	**0.625**	**2.2**	**0.2**
Ceratotherium	n	3		5		6		6		7	
	CS score	4	3.666667	3.8	2.8	3.83	3.33	3.833	3.5	4	2
	OR score	3.666667	3.33	3.25	2.5	3.2	2.4	3	3	3.14	2.43
	Mesowear score	**3.83**	**3.5**	**3.5**	**2.65**	**3.6**	**2.867**	**3.4**	**3.25**	**3.57**	**2.22**

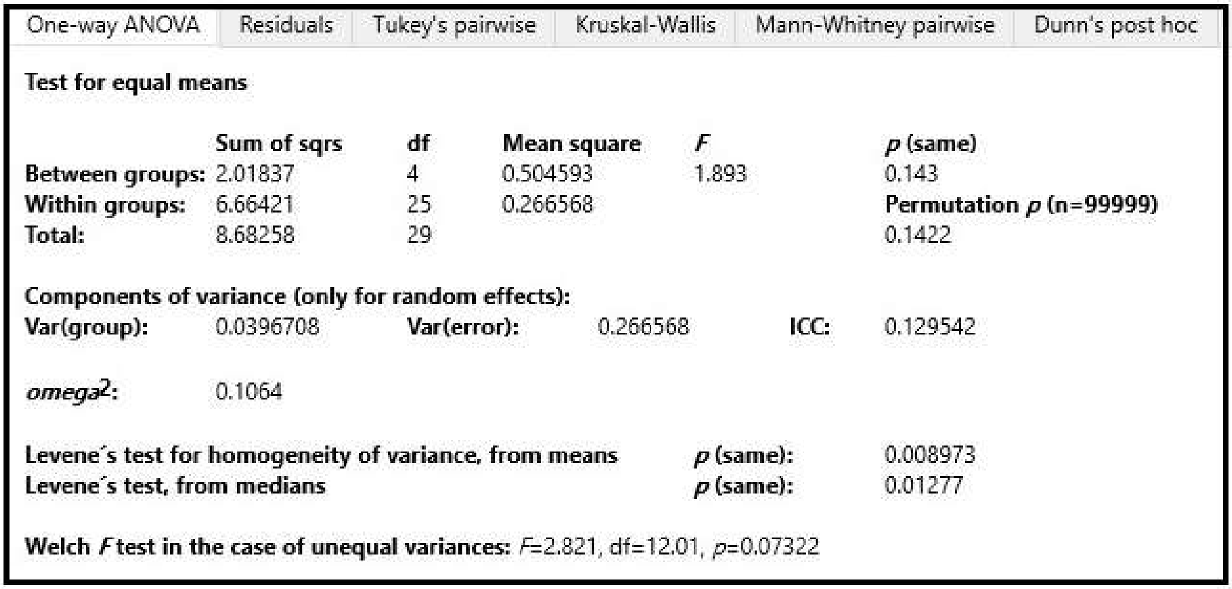
Table 5. The mean scores of cusp shape (CS), occlusal relief (OR) and the mean mesowear score for each tooth and cusp position for Diceros praecox and Ceratotherium mauritanicum using the mesowear method developed by Tylor et.al, 2013

4.1 STATISTICAL SIGNIFICANCE TEST



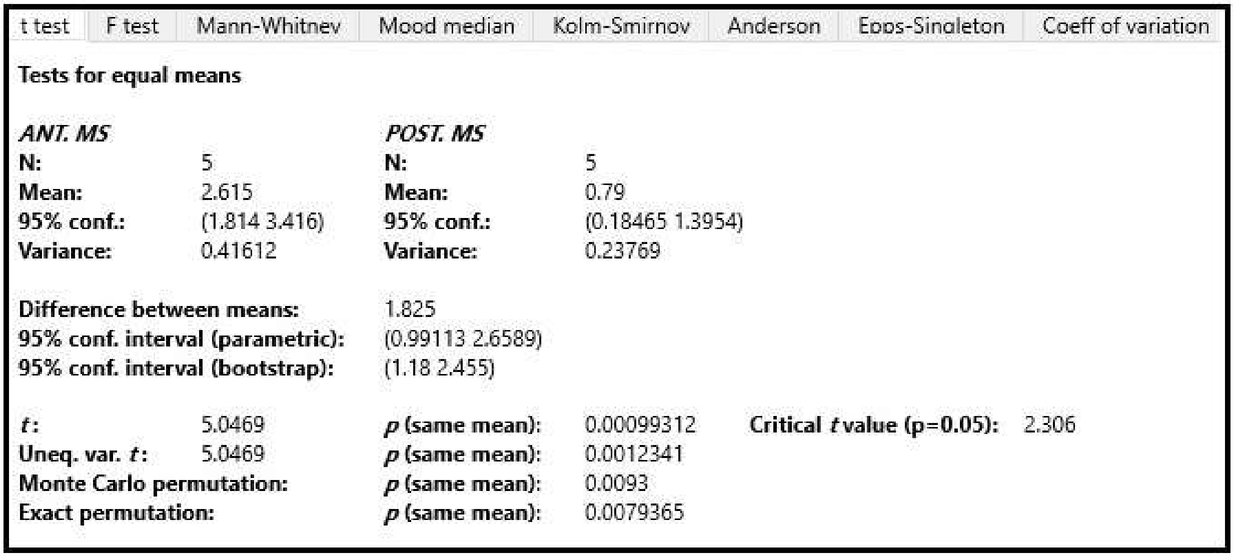
```
Tests for equal means

ANT. MS                                POST. MS
N:              5                      N:                  5
Mean:           3.581                  Mean:               2.8962
95% conf.:      (3.3813 3.7806)        95% conf.:          (2.2703 3.522)
Variance:       0.025862               Variance:           0.25406

Difference between means:              0.68476
95% conf. interval (parametric):       (0.13914 1.2304)
95% conf. interval (bootstrap):        (0.26762 1.0862)

t:              2.894                  p (same mean):      0.020074     Critical t value (p=0.05):   2.306
Uneq. var. t:   2.894                  p (same mean):      0.035651
Monte Carlo permutation:               p (same mean):      0.0228
Exact permutation:                     p (same mean):      0.015873
```

Figure 11. Statistical significance test (two sample t-test) summary of the cusp difference within each tooth position in Ceratotherium mauritanicum.



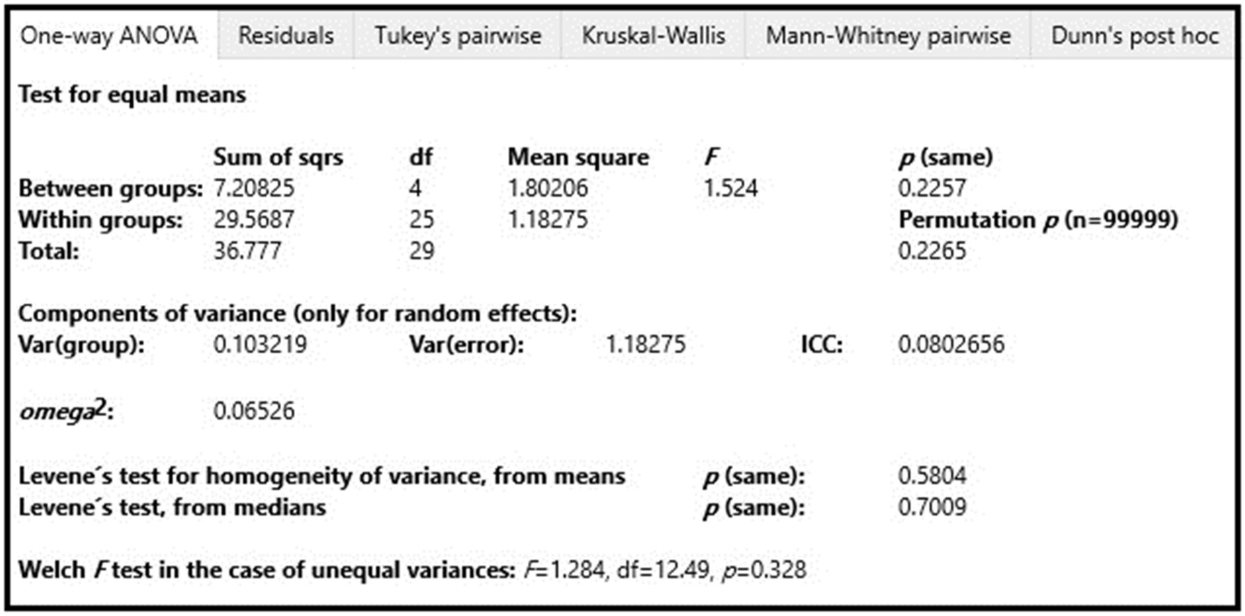
```
Test for equal means

                 Sum of sqrs    df     Mean square     F            p (same)
Between groups:  2.01837        4      0.504593        1.893        0.143
Within groups:   6.66421        25     0.266568                     Permutation p (n=99999)
Total:           8.68258        29                                  0.1422

Components of variance (only for random effects):
Var(group):      0.0396708      Var(error):      0.266568      ICC:  0.129542

omega2:          0.1064

Levene´s test for homogeneity of variance, from means      p (same):    0.008973
Levene´s test, from medians                                 p (same):    0.01277

Welch F test in the case of unequal variances: F=2.821, df=12.01, p=0.07322
```

Figure 12. Statistical significance test (One-Way ANOVA test) summary of tooth position difference in Ceratotherium mauritanicum.



```
Tests for equal means

ANT. MS                               POST. MS
N:               5                    N:              5
Mean:            2.615                Mean:           0.79
95% conf.:       (1.814 3.416)        95% conf.:      (0.18465 1.3954)
Variance:        0.41612              Variance:       0.23769

Difference between means:             1.825
95% conf. interval (parametric):      (0.99113 2.6589)
95% conf. interval (bootstrap):       (1.18 2.455)

t:               5.0469               p (same mean):  0.00099312     Critical t value (p=0.05):   2.306
Uneq. var. t:    5.0469               p (same mean):  0.0012341
Monte Carlo permutation:              p (same mean):  0.0093
Exact permutation:                    p (same mean):  0.0079365
```

Figure 13. Statistical significance test (two sample t-test) summary of the cusp difference within each tooth position in Diceros praecox.



```
Test for equal means

                 Sum of sqrs    df    Mean square    F           p (same)
Between groups:  7.20825        4     1.80206        1.524       0.2257
Within groups:   29.5687        25    1.18275                    Permutation p (n=99999)
Total:           36.777         29                               0.2265

Components of variance (only for random effects):
Var(group):      0.103219       Var(error):      1.18275     ICC:    0.0802656

omega2:          0.06526

Levene´s test for homogeneity of variance, from means   p (same):   0.5804
Levene´s test, from medians                              p (same):   0.7009

Welch F test in the case of unequal variances: F=1.284, df=12.49, p=0.328
```

Figure 14. Statistical significance test (One-Way ANOVA test) summary of tooth position difference in Diceros praecox.

In *Diceros* the anterior cusps of P2-P3 are more abrasion dominated with the mean mesowear score between 2.5 and 4 but most of the P4-M2 teeth show an intermediate wear pattern with the mean mesowear score between 1 and 3 and P2 shows the highest abrasion dominated wear pattern in the anterior cusp position (*Fig.15A*). In the posterior cusps of P2-P3 are more abrasion dominated than P4-M2 but M2 is the least abrasion dominated tooth in the posterior cusp position (*Fig.15B*).

In *Ceratotherium* the anterior cusps are more abrasion dominated than the posterior cusps and both the anterior and posterior P2 show highly abrasion dominated wear pattern than the rest of the teeth along the whole tooth row. *(Fig.15 C and D)*

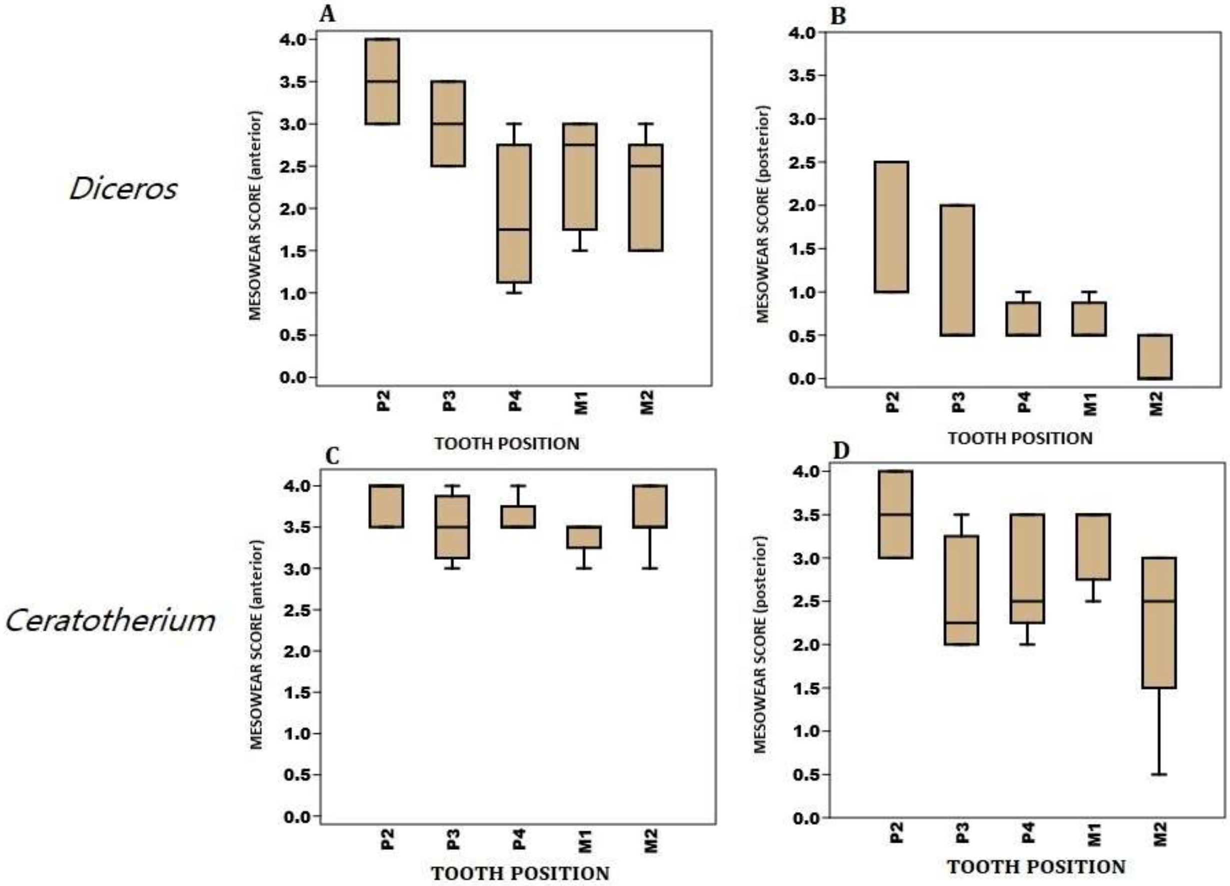


Figure 15. Box plots of the mesowear score of Diceros praecox (A and B) and Ceratotherium mauritanicum (C and D) scored from the anterior and posterior cusp positions. Each box represents 50% of the data with the median value and the whiskers representing 25% of the data.

4.2. DENTAL MESOWEAR SCORE OF *DICEROS PRAECOX*

The result obtained from the extended mesowear method for rhinos (EM(R)-S) analysis of the maxillary P2-M2 of *Diceros praecox* statistical significance test summary (One-way ANOVA test) in *Diceros praecox* indicate that there is no significant difference in each tooth position along the whole tooth row (p=0.2257) (*Fig.14)* though the Dunn's post hoc test showed that there is significant difference between P2 and M2 (p=0.04641) whereas the statistical significance test (two sample t-test) summary of the cusp position differences within each cusp (anterior and posterior) position in *Diceros praecox* indicate that there is significant difference between the anterior and posterior cusps (p=0.00099312) (*Fig.13)*.

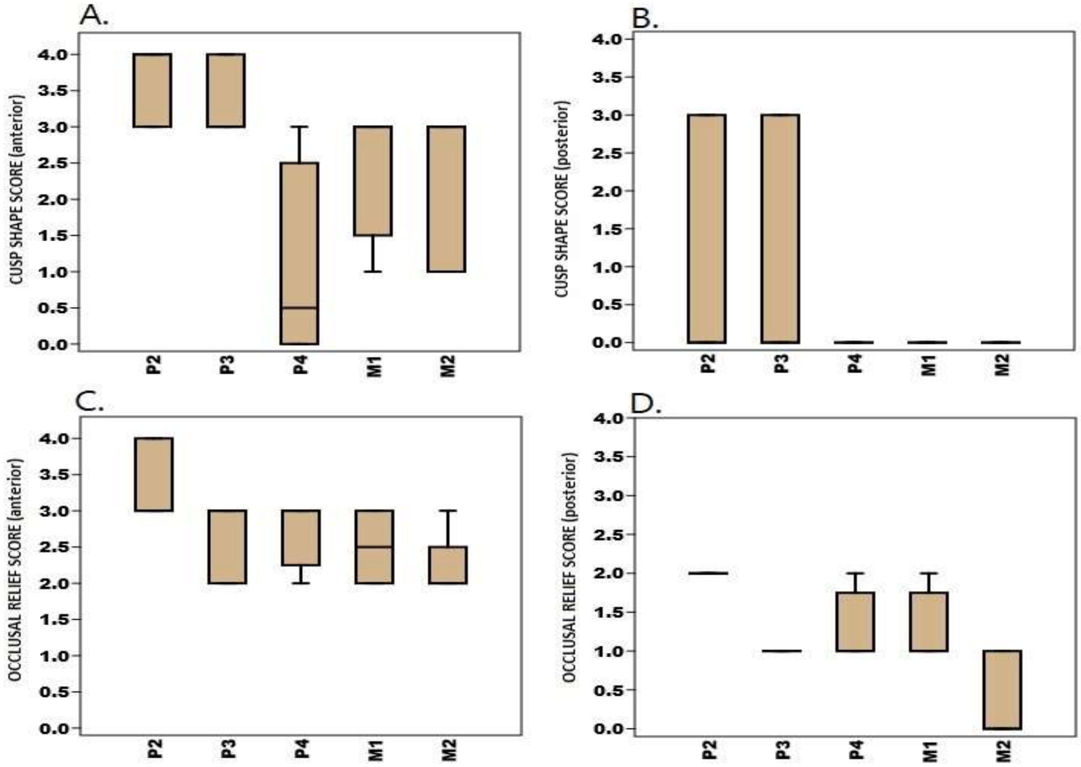


Figure 16. Box plots of the cusp shape score and occlusal relief score of Diceros praecox scored separately from the anterior and posterior cusp positions. Each box represents 50% of the data with the median value and the whiskers representing 25% of the data.

In *Diceros praecox* the anterior cusp of P2-P3 is between blunt and round-round whereas from P4-M2 is between round-sharp, round-round with very few sharp cusps *(fig.16 A).* The occlusal relief of the anterior cusps of P2-M2 are mainly between low and high-low *(fig.16 C).* The posterior cusps of P2-P3 is between sharp and round-round and from P4-M2 is exclusively dominated by sharp cusp *(fig.16 B).* The occlusal relief of P2 is high-low whereas from P3-M2 is between high and high-high *(fig.16 D).*

4.3. DENTAL MESOWEAR SCORE OF *CERATOTHERIUM MAURITANICUM*

The result obtained from the extended mesowear method for rhinos (EM(R)-S) analysis of the maxillary P2-M2 of *Ceratotherium mauritanicum* statistical significance test summary (One-way ANOVA test) indicate that there is no significant difference in each tooth position along the whole tooth row (p=0.143) *(Fig.12)* though the Dunn's post hoc test showed that there is significant difference between P2-P3 (p=0.04013) and P2-M2 (p=0.02247) whereas the statistical significance test (two sample t-test) summary of the cusp differences within each tooth position (anterior and posterior) in *Ceratotherium mauritanicum* indicate that there is significant difference between the anterior and posterior cusps (p=0.020074) *(Fig.11).*

In *Ceratotherium mauritanicum* the anterior cusp is dominated by blunt cusps (*Fig.17A)* and the posterior cusp of P2 is blunt, from P3-M1 is between blunt and round and M2 is between round-round and round-sharp (*Fig.17B)*. The occlusal relief of the anterior cusps of P2-M2 is between flat negative and low (*Fig.17C)* whereas the posterior is dominated by low and high-low (*Fig.17D).*

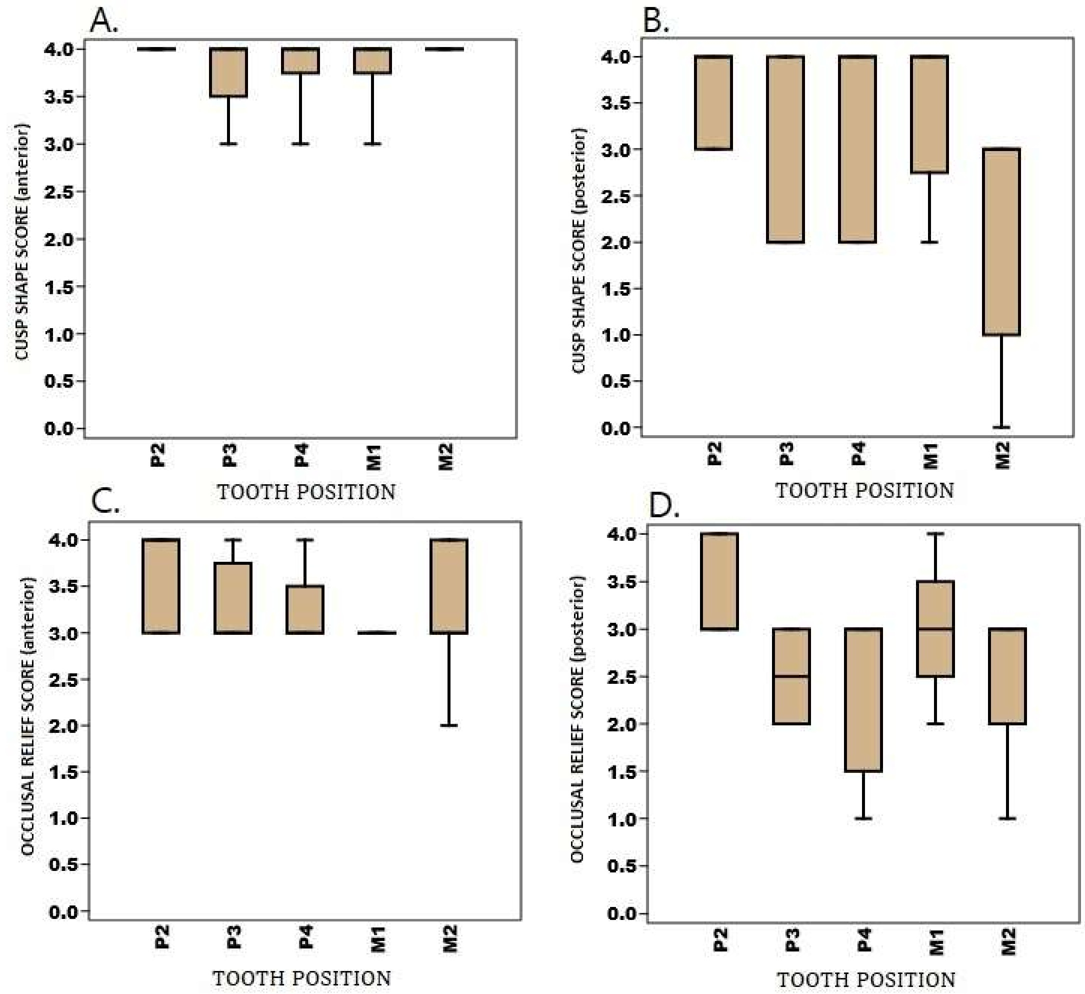


Figure 17. Box plots of the cusp shape score and occlusal relief score of Ceratotherium mauritanicum separately scored from the anterior and posterior cusp positions. Each box represents 50% of the data with the median value and the whiskers representing 25% of the data.

CHAPTER FIVE DISCUSSION

Though it is impossible to directly study past ecosystem, numerous methods and procedures have been devised that can be used to indirectly reconstruct a comprehensive paleoecological picture of fossil localities by combining many lines of evidence regarding the climate, vegetational structure, and fauna of a certain area at a specific time period (Croft et al., 2018)

Paleontologists study tooth wear patterns as these proxies provide important information about animals that lived in the past. Though there is no consensus among scientists about real cause of tooth wear in herbivores, various studies have been undertaken to infer their diet. The paleodietary adaptation of animal can be reconstructed based on the relative amount of abrasion and attrition produced on teeth as a result of their diet, determined by facet development on the buccal cusps. Browsers tend to have an attritive wear pattern whereas grazers have an abrasive wear patterns (Fortelius & Solounias, 2000). Previous studies of the living representatives of the two lineages *Diceros bicornis* (modern black African rhino), a browser and *Ceratotherium simum* (modern white African rhino), extreme grazer, have shown that there are significant differences between their dental-wear patterns.

Similarly different studies were conducted on the fossiliferous Hadar Formation to understand the paleoecological patterns at different time periods. In this chapter the result from the previous chapter (chapter-4) the implication on the paleodietary and paleoecology of the two Pliocene rhino species (*Diceros praecox and Ceratotherium mauritanicum)* was discussed in details, results from previous studies was compared and its relation with early hominin evolution at contemporaneous time period was discussed.

Ceratotherium mauritanicum and *Diceros praecox* are the only two rhino species currently recognized from Hadar. The two living African rhinocerotids, *Ceratotherium simum* and *Diceros bicornis* inhibit different habitat and dietary adaptation, their earliest representative would also assumed to have similar adaptation (Campissano, 2007). The majority of the collections are found in SH-1 submember but in other members there is no adequate sample size for the current study. Therefore, the paleodietary and paleoecological reconstruction of the rhinocerotids concentrate more on the lower Sidi Hakoma Member.

5.1. PALEODIETARY ADAPTATION AND PALEOECOLOGY OF THE TWO TAXONOMIC GROUPS

5.1.1. *Diceros praecox*

The mesowear score result of *Diceros praecox (fig. 15 A and B)* showed that a more attrition dominated tooth wear pattern was detected from P2-M2 both in the interior and posterior cusp positions along the whole tooth row. Tylor et.al, 2103 found similar result, however explained that the anterior cusps are relatively more abrasion dominated than the posterior cusps resulted from the asymmetry of rhino teeth, the anterior cusp is smaller than the posterior therefore can affect the mesowear result.

Though the symmetry of rhino teeth can affect the result of dental mesowear analysis and paved the way to raise questions about the adaptive importance of tooth symmetry and its effect on the development of dental mesowear patterns, it is morphological adaptation in lophodonts that having heterogeneous occlusal surface may facilitate the grinding up of heterogeneous browse (Tylor et.al., 2103).

When the anterior and posterior cusps of the entire tooth row is examined, the anterior cusp was significantly blunter and low relief than the posterior (Table 2 and figure 16). While comparing each tooth along the whole tooth row, P2-P3 are more abrasion dominated whereas from P4-M2 are relatively less abrasion dominated (Fig.16).

The result obtained from the extended mesowear method of rhino (*Diceros)* studied by Tylor et.al, 2013 shows almost similar score result with this study as it is shown by box plot in Fig.18, indicating the consistency of the method.

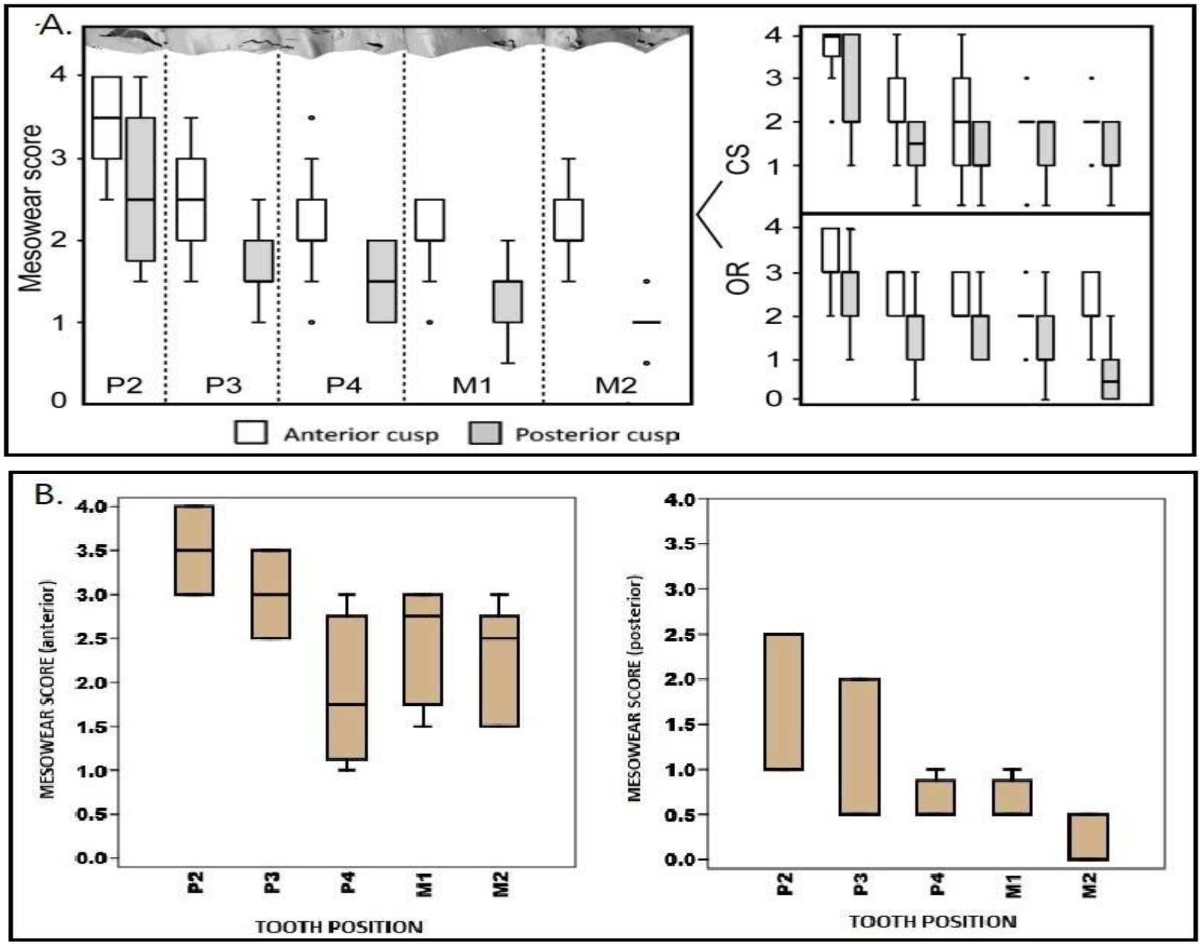


Figure 18. Comparison of the mesowear score result of D.bicornis (A) (Tylor et.al, 2013) and the mesowear score result of Diceros praecox from this study.

A negative tooth wear gradient was detected where tooth becoming less abrasion dominated from P2-M2. According to Tylor et.al, 2013, there are two possible reason for such gradient to be formed, tooth biomechanics and ingesta specific properties of abrasives. Higher bite force persistently exerted on the posterior teeth and transversal chewing movement as a result of jaw biomechanics. Ingesta specific abrasives in browsers like *Diceros* intraspecies tooth wear pattern is observed because environmental abrasives in the ingesta come first in to contact with the anterior teeth before the bolus is mixed and evenly distributed over the whole volume causing the anterior teeth to be more affected by the abrasives than the posterior teeth, it is typical of browsers like *D. bicornis* and mixed feeders like *D. unicornis*

Tylor et.al, 2013, stated that 'Due to the cusp and tooth position differences, the posterior M2 cusp provided scores analogous with the positions used so far in the literature to infer diet.' The cusp shape of the posterior M2 is mainly sharp and occlusal relief of between high and high-high is the characteristic feature of browsers (Fortelius & Solounias, 2000 & Tylor et.al, 2013).

The result from the mean score difference between captive and free-ranging ruminants and rhinoceros indicate that *Diceros bicornis* (the living African black rhino) is browser whereas *Ceratotherium simum* (the living African white rhinoceros) is a grazer *(Fig.*19) *(Tylor et.al. 2014).*

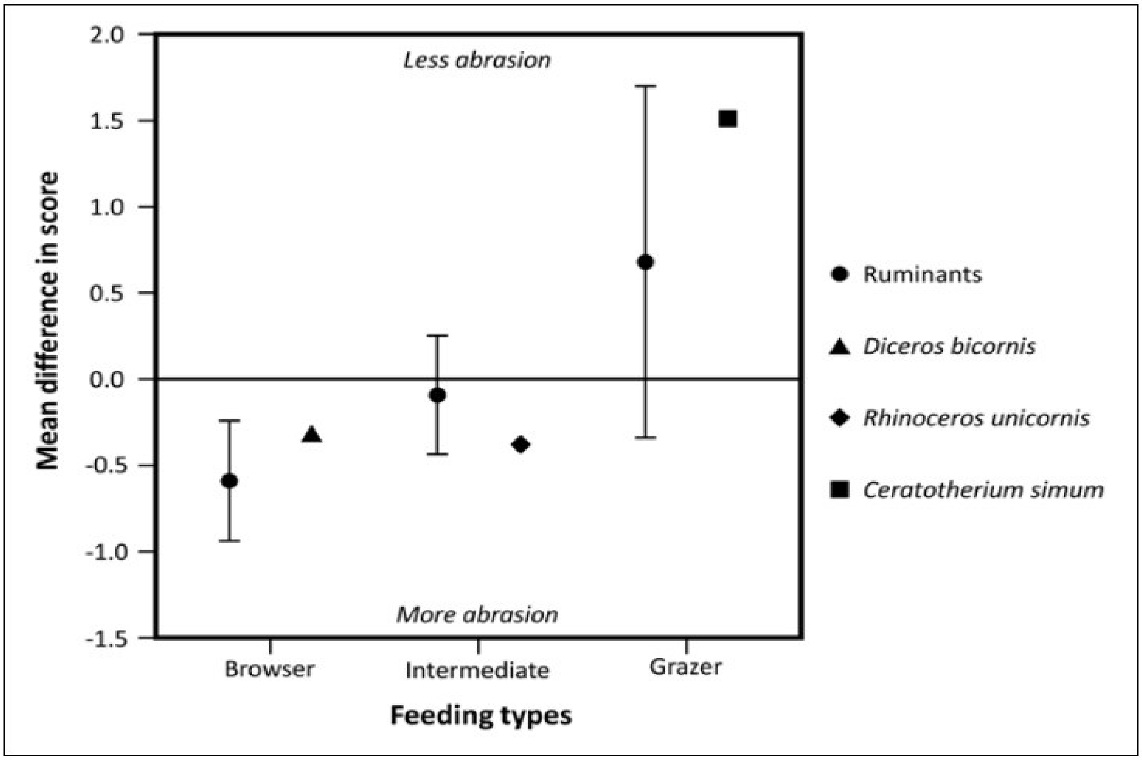


Figure 19. Comparison of the mean score difference between captive and free-ranging ruminants and rhinoceroses (free-ranging – captive) (Tylor et.al. 2014).

In Masai Mara Game reserve the study of the feeding and drinking habits of black rhinoceros revealed that there are 70 plant species from 30 botanical families were identified that are eaten by them though their primary choices are *Solanum incanum, Dichrostachys cinerea* and *Acacia* species and seen going in to salt licks for their mineral necessities like sodium, magnesium, potassium and calcium (Mukinya, 1977). Goddard, 1970, on the other hand observed them eating

102 species from 32 botanical families and selective of herbs, shrubs and noticeably legumes but their diet constitute very few amount of grasses.

Plant growth form	May to September 1971	October 1971 to February 1972	February to May 1972
Trees	47.4%	69.2%	49.8%
Herbs	40.8%	18.4%	35%
Shrubs	6.1%	11.6%	14.%
Others	5.2%	2.2%	3.9%
Total	99.5%	101.4%	103.2%

Table 6. Plant growth forms eaten by black rhinoceros at different seasons in Masai Mara Game Reserve (Mukinya, 1977).

Stable carbon isotope data from faeces collected over a variety of spatial and temporal scales from the semi-arid savanna of the Kruger National Park, South Africa, to test dietary predictions for African ungulates along the browser/grazer (or C3/C4) continuum indicate that C. simum shows 90% C4 grass and Diceros bicornis shows that only 9% C4 grasses (Codron et. al., 2007). C3 vegetation includes fruits, leaves, tree roots, bushes, and forbs whereas C4 vegetation includes tropical grass glades, seeds, and roots (Campisano, 2007). The result from feeding track method study of the feeding habit of black rhinoceros on the other hand revealed that four groups of plant species were identified. These are woody plants consisting trees and shrubs with woody stems like *Colophospermanum mopane* or *Catophractes alexandri*; Dwarf shrubs like *Indigofera adernocarpa* or *Tephrosia oxygona*; Succulent plants like *Euphorbiacea* and *Zygophylum simplex* and hebs **(**Hennig & Gindrig, 2001).

5.1.2. *Ceratotherium mauritanicum*

The dental mesowear score result of this study indicate that both the anterior and posterior cusps show an abrasion tooth wear pattern though the anterior is more abrasion dominated than the posterior. The score result also show blunt shape and low relief, the characteristic feature of grazers (Tylor et.al, 2013).

Unlike *Diceros*, *Ceratotherium* do not show tooth wear gradient along the tooth row rather a uniform wear pattern is detected. The absence of wear gradient in Ceratotherium indicate that factors responsible for the formation of tooth wear gradients in browsers like Diceros , jaw biomechanics and bolus formation sequence along the tooth row, are masked by the high abrasion formed in *Ceratotherium* (Tylor et.al, 2013).

According to (Tylor et.al, 2013) the possible reason for the absence of teeth gradient in *Ceratotherium* unlike the browse diets, grass diets contain significant amount of abrasive elements enough to create high abrasion and this indicate that there is no dental functional differentiation, evolutionary adaptation for the formation of less specialized premolars which could finally led for the development post canine homodonty.

The result obtained from the extended mesowear method of rhino (*Ceratotherium)* studied by Tylor et.al, 2013 shows almost similar score result with this study as it is shown by Box plot in Fig.20.

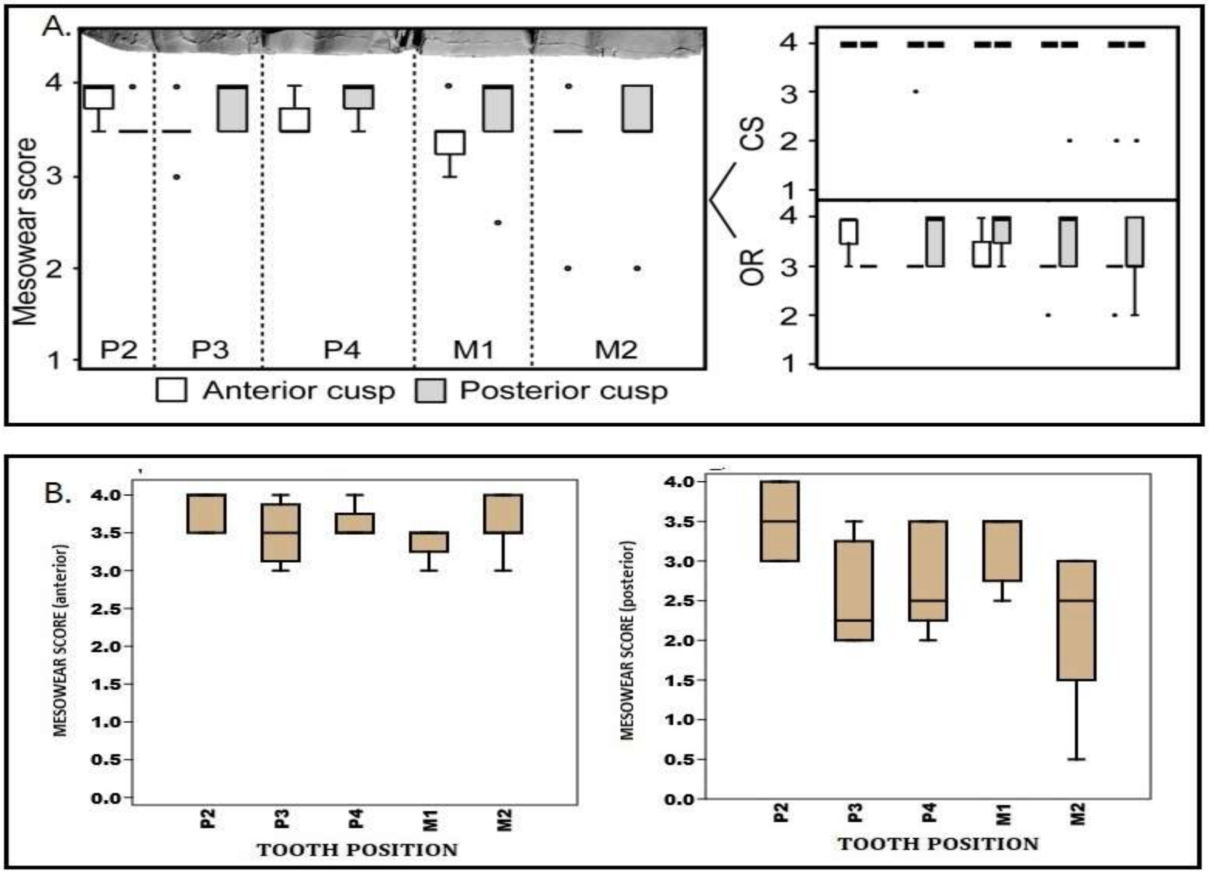


Figure 20. Comparison of the mesowear score result of C. simum (A) (Tylor et.al, 2013) and the mesowear score result of Ceratotherium mauritanicum from this study (B).

5.2. IMPLICATION TO HOMININ ENVIRONMENTS AND EVOLUTION

According to (Faith et al. 2019), megaherbivores are ecosystem engineers and they have the potential of modifying the biotic communities enough to affect a wide diversity of species implicating that the great majority of early human evolution that took place in the context of ecosystems are different from those known today. As a result, it is unknown to what extent the ecosystems of the present are indicative of those of the past, despite the baseline for reconstructing the ecological setting of human evolution is provided by the current ecosystem, and testing the hypothesis needs to understand the ancient biological communities that lived together with our ancestors.

Based on (Levin, 2015), human evolutionary study is fundamentally concerned with understanding how humans evolved and interacted with their environments and requires understanding the evolution of the variety of anatomical and behavioral traits that are believed to distinguish humans from other species including terrestriality, bipedalism, dietary flexibility, tool use, Omnivory, larger brains, long-distance migrations, and the birth of dependent children and their adaptive significance. Moreover, environment has played the major role in most of the changes in human evolution like transition from arboreal to terrestrial behaviors, bipedalism etc… that are considered in terms of local or regional environmental factors, such as vegetation, water balance, temperature, shadow, climate and landscape stability, topographic shift, temperature, the presence of lakes as well as interspecific competition, community dynamics, fire, seasonality, and plant herbivore dynamics and so on.

According to (Reed, 2013), reconstructing the African Pliocene ecosystem and vegetation structure of early Pliocene hominin requires understanding the present environment as well as the living mammalian communities. For instance, using faunal approach of fossil mammals found in association with early hominins in the same deposit can answer questions related to evolutionary paleoecology and most studies on reconstructing the African hominin paleoecology uses this method to infer paleohabitat.

The extant African habitats are frequently used to construct the paleohabitats based on the principle that the basic structures of the ancient and the present habitat is the same (Reed, 2013). For instance, in East Africa the presence of volcanic or volcano-clastic sediments and well known relation between the stratigraphic and fossil bearing layers as well as numerous multidisciplinary studies produced a large body of geological, paleontological, paleobotanical, and taphonomic evidence have made it possible for reconstructing the paleoenviroment and dating the hominid and related faunal assemblages with greater accuracy (Boaz, 1977) and there have been definite, long-term trends in favor of more open environment over the last10 million years despite the variation in the spatial and temporal distribution (Levin, 2015).

According to (Campisano, 2007), *Australopithecus afarensis* is the only taxa represented below the Bousidima disconformity and consistently existed throughout the whole sequences whereas Homo is found above the disconformity but no Hominins are discovered from the Basal and Sidi Hakoma Tuff sub-members and each sub-member constitutes an average hominids between 2.5-4.5%. They are most abundant in SH-1 (8%) and KH-1 (6.6%) but their low proportion is recorded in SH-2 (1.7%) from the total assemblages of fossil specimens collected in Hadar. According to tests of relationship with other taxa in addition to spatial distribution over an area with a specific geomorphology, macroclimate, soil and vegetation pattern and associated fauna, there isn't much evidence to suggest that A. afarensis has a special predilection for any particular habitat.

Early hominins adopted a variety of terrestrial bipedality, and certain taxa's arboreal activity likely persisted as a significant component of their locomotor behavior for millions of years. For instance, despite being a walking upright Australopithecus afarensis, Lucy exhibited more arboreal behavior than either modern humans or Homo erectus (Kappelman et.al. 2016). *A. afarensis* can be generally characterized as a habitual biped and survived both terrestrial and arboreal environment (Campisano, 2007).

Carbon isotopic analysis of (Wynn et.al, 2013 & 2016), has revealed that there was substantial dietary shift in hominins in the middle Plioicene, which was evidenced by the increase in C4 diet in Australopithecus. The dietary analysis of Austaralopithecus afarensis in Hadar also indicate that they are generalist Omnivore that consume food obtained from different sources in time and space. The sources include grass seeds and roots seasonally, sedge underground storage organs at other times, termites, succulent CAM plants, and even small game or scavenged carcasses

In any *A. afarensis* localities including Hadar a mosaic of habitats including woodlands (both open and closed), gallery forests, edaphic grasslands, and more open/arid grasslands and shrublands are available (Campisano, 2007).

CHAPTER SIX CONCLUSION AND RECOMMENDATIONS

6.1. CONCLUSION

The fossiliferous hominin bearing Pliocene Hadar Formation located in North-Eastern Ethiopia of Lower Awash Valley is one of the renowned paleontological site with exceptional fossil mammal specimens including hominins like *Australopithecus afarensis* (Lucy). A wide ranges of studies have been undertaken in Hadar in order to reconstruct the paleodietary adaptation of different mammalian groups and the past ecosystem of this specific site using different approaches like Ecomorphology, Palynology, Isotopic analyses of the biogenic carbonates, herbivore dental mesowear and microwear analysis, faunal abundance and so on. However, there is few or no data from dental mesowear analysis of the Pliocene rhinocerotids. Therefore; the present study tries to reconstruct the paleodietary adaptation and the past ecological context of the Hadar Formation of the Sidi Hakoma member using dental mesowear analysis of *Diceros praecox and Ceratotherium mauritanicum* fossil tooth specimens.

The different shapes observed on the enamel edges of molars and the amount of abrasion and attrition are as a result of differences in diets consumed by species and therefore important in constructing Paleodiets (Hernesniemi et al., 2011).

According to (Tylor 2013), the various wear patterns in the cusp positions can be a result of their morphological adaptation to a certain dietary ecology. The anterior cusps of *D. bicornis,* a browser, consistently exhibit abrasion-dominated wear patterns, with teeth becoming less abrasive from P2-M2, which helps to facilitate crushing the heterogeneous food (browse). This can be explained by the jaw mechanics, in which the posterior teeth provide a strong biting force and smaller, more frequent transverse movements that are precisely tied to the qualities of the food being eaten. *C.simum* on the other hand, is a grazer in which the anterior and posterior cusps exhibit similar wear patterns that make easier to homogeneous grasses. Contrary to browsers, grazers have higher rates of abrasive ingesta than other signals, which tend to produce uniform wear patterns throughout the tooth row and may be the initial step in the evolution of homodonty.

Dental mesowear studies the facets developed on the occlusal morphologies of herbivore tooth via cusp relief and shape in order to categorize them according to their dietary preferences based on the observed gross dental wear patterns. The rate of facet development provides the relative proportion of attrition (tooth to tooth contact) and abrasion (tooth to food contact). Reconstruction of their dietary adaptation can provide us essential information about their habitat as well as other communities living associated with them.

According to Dental mesowear method, grazers exhibit high percentage of attrition-dominated wear pattern, low relief and blunt cusps whereas, browsers exhibit high percentage of abrasion-dominated wear pattern with high relief and sharp cusps (Fortelius and Solounias, 2000). The basic principle of this approach is that browsers ingesta contain very few abrasive components that are unable to create relatively significant wear on the occlusal surface of tooth while grazers often feed on grasses and low growing plants they ingest abrasive components that are incorporated with their diet that are capable of creating wear.

Result from the extended dental mesowear analysis of the two taxa, *Diceros praecox and Ceratotherium mauritanicum,* collected from the Sidi Hakoma member of Hadar Formation show different dietary preference. In the literature the posterior M2 is used so far to infer diet (Tylor et.al. 2013). Hence the dietary preference of the two lineages is inferred according to the current working principles.

The result obtained from the dental mesowear analysis of *Diceros praecox* indicates that the anterior cusps are more abrasion dominated than the posterior or the posterior cusps are more attrition dominated than the anterior cusps detected along the whole tooth row. The posterior cusp of M2 shows attrition dominated tooth wear pattern with high relief and sharp cusps typical of browsers. The mesowear score result of *Ceratotherium mauritanicum* on the other hand indicates that both the anterior and posterior cusps show abrasion dominated tooth wear pattern though the anterior is more abrasion dominated than the posterior attributed to abrasive diets. The posterior M2 cusp shows between ‘round-round’ and ‘round-sharp’ and low and high-low. The general mesowear score result suggested that *Ceratotherium mauritanicum* is a grazer.

Stable carbon isotope data from faeces collected over a variety of spatial and temporal scales from the semi-arid savanna of the Kruger National Park, South Africa, to test dietary predictions for African ungulates along the browser/grazer (or C3/C4) continuum indicate that *C. simum* shows 90% C4 grass and *Diceros bicornis* shows only 9% C4 grasses (Codron et. al., 2007). C4 vegetation includes tropical grass glades, seeds, and roots (Campisano, 2007). The result from feeding track method study of the feeding habit of black rhinoceros on the other hand revealed that four groups of plant species were identified. These are woody plants, Dwarf shrubs, Succulent plants and hebs (Hennig & Gindrig, 2001).

The habitat conditions of the Sidi Hakoma sub-members are, bushland, woodland, shrub land, closed woodland and ecotone in SH-1 sub-member. Bushland, woodland, shrub land, woodland, Grassland and ecotone in SH-2 sub-member. Bushland, shrub land, grassland and ecotone in SH-3 sub-member and bushland, woodland, shrub land, Grassland and ecotone in SH-4 sub-member (Table 6). Generally all sub-members of the Sidi Hakoma member showed almost similar habitat type. Therefore, the habitat of Sidi Hakoma member, Hadar formation can be described as a mosaic of habitats ranging from bushland, woodland, shrub land, Grassland to ecotone.

The present study shows that the Hadar fossil specimen of *Diceros praecox* was a browser that may feed on leaves**,** shoots**,** tree bark**,** or fruits from plants whereas, *Ceratotherium mauritanicum* is grazers which feed on grass and other low-growing vegetation and these diets represent a wide ranges of habitats. Based on the result obtained from this study it is possible to conclude that Sidi Hakoma member of Hadar constituted a mosaic of habitats ranging from a more open habitats, wooded to treeless savanna and ecotone, which is revealed from the reconstructed Paleodietary adaptation of the two Pliocene rhinocerotid lineages is almost similar with previous studies conducted on both fossil and extant taxa.

Fossil hominin mainly *Australopithecines* are recovered from the different members of the Hadar including Sidi Hakoma member and as they inhibited the same environment they are believed to have experienced the same climatic and environmental conditions.

6.2. RECOMMENDATIONS

- ❖ Either collection preference (collection bias) or Taphonomic process members other than the Sidi Hakoma member do not contain samples enough to make inference. As a result; this study focuses only on the rhinocerotid specimens collected from Sidi Hakoma member of Hadar Formation. Hence collecting specimens from the whole sequences could provide us better understanding about their spatial and temporal dietary adaptation as well as evolutionary ecology.

- Most rhinocerotid specimens in Hadar are not identified at the lower taxonomic unit rather they are simply assigned as rhinocerotidae (figure 18). Different species found in the same group may have distinct feeding behavior. For example both *Diceros praecox* and *Ceratotherium mauritanicum* are included in rhinocerotid group but *Diceros praecox* is a browser and *Ceratotherium mauritanicum* is a grazer. Therefore; identifying the specimens at the lowest taxonomic unit will help us to understand the dietary adaptation and related phenomena of a particular units.
- There hasn't been enough studies undertaken on the Hadar rhinocerotids in order to reconstruct their paleodiet and Paleoecology using different approaches. Therefore; if more studies are conducted using different approaches, the combined result will provide evidences that will enable us to draw better and more reliable conclusions.

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Appendix 1. The dental mesowear score result of *Diceros praecox*

specimen number	*Taxa*	Element	cusp shape Anterior	cusp shape Posterior	Occlusal relief anterior	posterior Occlusal relief	stratigraphy
AL.126-21A	*Diceros praecox*	URP2	blunt	sharp	flat negative	high-low	Sidi Hakoma member (SH-1)
AL.126-21B	*Diceros praecox*	ULP2	blunt	sharp	low	high-low	Sidi Hakoma member (SH-1)
AL.384-1B	*Diceros praecox*	ULP2	blunt	round-round	low	high-low	Sidi Hakoma member (SH-4)
AL.126-21A	*Diceros praecox*	URP3	round-round	sharp	low	high	Sidi Hakoma member (SH-1)
AL.126-21B	*Diceros praecox*	ULP3	round-round	sharp	high-low	high	Sidi Hakoma member (SH-1)
AL.384-1B	*Diceros praecox*	ULP3	blunt	sharp	low	high	Sidi Hakoma member (SH-4)
AL.126-21A	*Diceros praecox*	URP4	sharp-round	sharp	low	high	Sidi Hakoma member (SH-1)
AL.126-21B	*Diceros praecox*	ULP4	round-round	sharp	low	high	Sidi Hakoma member (SH-1)
AL.384-1A	*Diceros praecox*	URP4	sharp	sharp	high-low	high-low	Sidi Hakoma member (SH-4)
AL.384-1B	*Diceros praecox*	ULP4	sharp	sharp	low	high	Sidi Hakoma member (SH-4)
AL.126-21A	*Diceros praecox*	URM1	round-round	sharp	low	high	Sidi Hakoma member (SH-1)
AL.126-21B	*Diceros praecox*	ULM1	round-round	sharp	low	high	Sidi Hakoma member (SH-1)
AL.384-1A	*Diceros praecox*	URM1	sharp-round	sharp	high-low	high	Sidi Hakoma member (SH-4)
AL.384-1B	*Diceros praecox*	ULM1	round-round	sharp	high-low	high-low	Sidi Hakoma member (SH-4)
AL.126-21A	*Diceros praecox*	URM2	round-round	sharp	low	high-high	Sidi Hakoma member (SH-1)
AL.126-21B	*Diceros praecox*	ULM2	sharp-round	sharp	high-low	high	Sidi Hakoma member (SH-1)
AL.313-1	*Diceros praecox*	URM2	round-round	sharp	high-low	high-high	Denen Dora (DD-2)
AL.384-1A	*Diceros praecox*	URM2	round-round	sharp	high-low	high-high	Sidi Hakoma member (SH-4)
AL.384-1B	*Diceros praecox*	ULM2	round-sharp	sharp	high-low	high	Sidi Hakoma member (SH-4)

Appendix 2. The dental mesowear score result of *Ceratotherium mauritanicum*

specimen number	Taxa	Element	cusp shape anterior	cusp shape posterior	Occlusal relief anterior	Occlusal relief posterior	stratigraphy
AL.125-1	*Ceratotherium mauritanicum*	ULP2	blunt	blunt	flat negative	flat negative	Sidi Hakoma member (SH-1)
AL.137-28B	*Ceratotherium mauritanicum*	URP2	blunt	blunt	flat negative	low	Sidi Hakoma member (SH-1)
AL.180-2	*Ceratotherium mauritanicum*	URP2	blunt	blunt	low	low	Kada Hadar (KH-2)
AL.125-1	*Ceratotherium mauritanicum*	URP3	blunt	round	low	high-low	Sidi Hakoma member (SH-1)
AL.125-1	*Ceratotherium mauritanicum*	ULP3	blunt	round	flat negative	low	Sidi Hakoma member (SH-1)
AL.129-25	*Ceratotherium mauritanicum*	ULP3	blunt	blunt			Sidi Hakoma member (SH-1)
AL.137-28A	*Ceratotherium mauritanicum*	ULP3	blunt	blunt	low	low	Sidi Hakoma member (SH-1)
AL.137-28B	*Ceratotherium mauritanicum*	URP3	blunt	round	low	high-low	Sidi Hakoma member (SH-1)
AL.125-1	*Ceratotherium mauritanicum*	URP4	blunt	round	low	low	Sidi Hakoma member (SH-1)
AL.125-1	*Ceratotherium mauritanicum*	ULP4	blunt	round	low	high-low	Sidi Hakoma member (SH-1)
AL.129-25	*Ceratotherium mauritanicum*	URP4	blunt	blunt	flat negative	low	Sidi Hakoma member (SH-1)
AL.129-25	*Ceratotherium mauritanicum*	ULP4	blunt	blunt			Sidi Hakoma member (SH-1)
AL.137-28B	*Ceratotherium mauritanicum*	URP4	blunt	blunt	low	high	Sidi Hakoma member (SH-1)
AL.235-3	*Ceratotherium mauritanicum*	URP4	blunt	blunt	low	low	Sidi Hakoma member (SH-1)
AL.125-1	*Ceratotherium mauritanicum*	URM1	blunt	blunt	low	low	Sidi Hakoma member (SH-1)
AL.125-1	*Ceratotherium mauritanicum*	ULM1	blunt	blunt	low	low	Sidi Hakoma member (SH-1)
AL.129-25	*Ceratotherium mauritanicum*	URM1	blunt	blunt			Sidi Hakoma member (SH-1)
AL.129-25	*Ceratotherium mauritanicum*	ULM1	blunt	blunt	low	low	Sidi Hakoma member (SH-1)
AL.137-28A	*Ceratotherium mauritanicum*	ULM1	blunt	blunt	low	flat negative	Sidi Hakoma member (SH-1)
AL.137-28B	*Ceratotherium mauritanicum*	URM1	blunt	ound - round	low	high-low	Sidi Hakoma member (SH-1)
AL.125-1	*Ceratotherium mauritanicum*	URM2	blunt	harp - round	low	low	Sidi Hakoma member (SH-1)
AL.125-1	*Ceratotherium mauritanicum*	ULM2	blunt	harp - round	low	high-low	Sidi Hakoma member (SH-1)
AL.129-25	*Ceratotherium mauritanicum*	URM2	blunt	ound - round	flat negative	low	Sidi Hakoma member (SH-1)
AL.129-25	*Ceratotherium mauritanicum*	ULM2	blunt	ound - round	flat negative	high-low	Sidi Hakoma member (SH-1)
AL.137-28B	*Ceratotherium mauritanicum*	URM2	blunt	arp	high-low	high	Sidi Hakoma member (SH-1)
AL.235-3	*Ceratotherium mauritanicum*	URM2	blunt	ound - round	low	low	Sidi Hakoma member (SH-1)
AL.235-3	*Ceratotherium mauritanicum*	ULM2	blunt	ound - round	low	low	Sidi Hakoma member (SH-1)