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Sercan Acar

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PREFACE

The diet of early species is still controversial because the environmental and climatic changes in the Pliocene are one of the most problematic and very interesting issues. How was the effect it's on dietary structure and the masticatory anatomy of early species? The climatic change is a key factor in occurrence of habitat. Together with these changes, which are the reduced rainfall and cooler temperatures or from forest to savanna, the habitat of the early hominids was shifted so their feeding ground was changed. In other respects, the masticatory morphology of Ardipithecus, Australopithecus and Paranthropus is affected directly or indirectly by these variations. In addition, these variations are changing based on the environment and the habitat i.e. the quality of food sources and type of food consumed, and reflect on the size/shape of the early hominids teeth.

CHAPTER 1

THE PLIOCENE PERIODS' HOMINIDS

There were appeared early human species in the plio-pleistocene period, among them *Ardipithecus, Australopithecus* and *Paranthropus* species. Ardipithecus ramidus was found in the Middle Awash area of Ethiopia. It is estimated that *Ardipithecus ramidus* inhabited in forests/closed woodland in between 5.6 (first appearance date) - 4.4 million years ago (last appearance date), when the early hominid specimens were observed. When the crania dental characters of Ardipithecus ramidus were examined, it was sited between Australopithecus afarensis and chimpanzees. For example, the canine's and molar's enamel thickness of

Ardipithecus ramidus is thinner than that of Au. afarensis. Nevertheless, Ardipithecus ramidus' canines are bigger than those of Au. afarensis (White et al. 1994). In general, the molars size of Ardipithecus ramidus is small and similar to one another, but their canine is not as big as Australopithecus specimens. The reason lies in their diet or habitat (soft or non-abrasive items). Ardipithecus ramidus' tooth structure looks like an omnivore (Suwa et al. 2009).

Australopithecus anamensis was found in the Kanapoi region of East Lake Turkana in Kenya (open woodland), and dated 4.2-3.8 Ma. Their tooth morphology shows that some of Au. anamensis tooth characters are different from one another, while some of their tooth features are similar with that of Au. afarensis. The upper jaw teeth of Au. anamensis indicate that the crown enamel thickness of Australopithecus anamensis is similar to that of Australopithecus afarensis. For this reason, their canine enamel tends to be thick. When the enamel thickness is compared between Au. anamensis and Ardipithecus ramidus, the enamel thickness in Australopithecus anamensis is thicker than Ardipithecus ramidus, with a large molar in buccolingual, due to their diet.

Australopithecus afarensis lived in Hadar, about 3.8-2.9 million years ago. Hadar is one of the major areas, in terms of variety of sources, which reflects their tooth structure (mosaic shape). According to dental microwear of Au. Afarensis, they ate soft foods like fruits. However, tooths size and shape show that they could have also eaten hard like roots and nuts. On the other

hand, their enamel is thick. According to Jolly (1970), thick enamel is dominant in the early specimens (Australopithecus and Paranthropus) because of their diets or habitats (closed/ open woodlands, bushlands and edaphic grasslands).

Australopithecus africanus have been discovered in South Africa, such as Sterkfontein, Makapansgat and Taung, and dated 3.3 and 2.1 Ma. Au africanus' tooth morphology generally shows that their incisors sizes are almost the same in the medial and lateral part. Au. africanus had large molar and premolar, like Paranthropus, and also covered in thick enamel. Next, the mandibular structure of Australopithecus africanus was huge in shape together with primitive corpus. Their diets consisted of also soft and hard foods like fruit, plants, nuts, seeds etc.

Paranthropus boisei was discovered in many locations, such as Olduvai George, Peninj, Chesowanja, west Turkana, Koobi Fora and Omo, in Plio-Pleistocene and generally, these locations had warm, dry, open and savanna woodland flora habitat. It was dated 2.3 and 1.4 Ma. Paranthropus boisei is the strongest specimens, in comparison to other specimens. Their craniofacial morphology was very robust and powerful, as well as the biggest and flattest cheek teeth (Kay, 1985; Grine and Martin, 1988). Paranthropus boisei's dental morphology is wide-based, major-crowned and of the thickest enamel, when compared to other hominids, in terms of post-canine (Wood and Constantino, 2007). Furthermore, their tooth crowns in appearance enlarge at a quicker proportion than in any hominid (Beynon& Wood, 1987). Moreover, when the mandible and

post-canine are compared between Paranthropus boisei and other specimens, Paranthropus boisei is hugely-structured and their mandibular height and width proportion are parallel to each other. Those features indicate that their diet was consisted tough foods like nuts and roots. However, the microwear patterns of Paranthropus boisei are more similar to soft or fruit eaters. It may more diverse and wider diet for Paranthropus boisei (Ungar et al., 2008).

Paranthropus robustus was found in Kromdraai, Swartkrans, Drimolen, Gondolin and probably Sterkfontein (Africa, with open woodland and savannah), and dated in between 1.8 and 1.2 Ma. In general, their premolar and molar shape are hugely-structure, when compared to Australopithecus specimens, and their canine and incisors sizes. Furthermore, Paranthropus robustus' mandibular structure is huge and in a cross-sectional shape. Their enamel is thick (post-canine) like Paranthropus boisei. Like Paranthropus boisei, they were not just eaten tough foods like nuts and roots. Their diet was more diverse and wider, ate fruit, seeds, leave, insects etc. (Sponheimer et al., 2006).

1.1. The Habitats and Diets of Early Species

The environmental choices of the early hominids are poorly understood, although, much argument of the hominid evolution is associated with habitat-specific conditions (e.g., Jolly, 1970). However, this situation is should be related to their diet. The main point of diet depends on the implement of feasible pattern

of early hominin evolution and natural factors like ecology, habitat, due to trophic effects bear. It has a direct relation with the generation of the masticatory anatomy, as the relationship between skeletal muscle improvements and food items acquirement. Therefore, the importance of the diet in the Plio-Pleistocene hominid is clearly seen. In a similar way, the dental morphology and diet-inclined features, and design seem to be heavily associated with food items consistency. In other ways, all factors are closely related to one another.

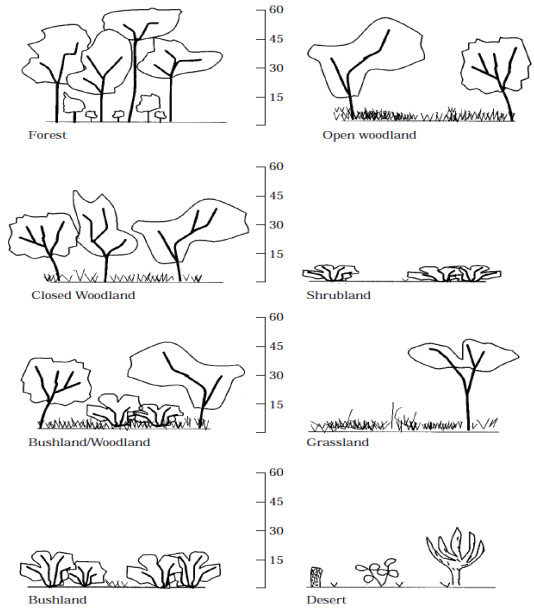

Figure 1. *Samples of habitat types (from fig 3, Reed, 1997)*

According to WoldeGabriel et al. (1994), the earliest species *Ardipithecus ramidus* is seen to have lived in closed woodlands,

in Aramis like in the above *figure 1*. This opinion is also supported by the stable isotopic analysis and other analyses, that is to say, *Ardipithecus ramidus* was not seen in the open savanna, as their environmental conditions were moist and colder, including habitats ranging from woodland to forest (WoldeGariel et al., 2009). It is thought that there is no evidence to associate *Ardipithecus ramidus* with more open-wooded grasslands or savanna (White et al., 2009). However, together with recent studies in that, Aramis is represented by bush savanna or tree with 25% or less woody canopy cover. It is probably ranged from the riparian forest to grassland. The diet of *Ardipithecus ramidus* was fresh leaves and soft fruits in woodland locations, so their enamel was, unlike those carnivorous, thin. On the contrary, *Australopithecus* had thick enamel. This situation demonstrates that they used to feed on hard items. Furthermore, the similar situation is also seen in the upper Miocene hominoids. Observers supported that early specimens ate abrasive and strong items, and for this reason their enamel was thick. Nevertheless, with other findings on *Ardipithecus ramidus*, this theory is declined by observers, due to major evidence. It is predicted that *Ardipithecus* was thin in enamel. As a consequence, their diet included soft and non-abrasive food items.

The habitat in *Australopithecus* diets is comprised of soft food items, such as fruits, hard smaller fruits, so they did not need very large incisors for hulling certain items or anything that required large preparation, or possibly underground storage

organs (USOs) like, rhizomes and roots (Teaford and Ungar, 2000, see also Hatley&Kappelman 1980). It has not been seen that the Pliocene period' *Australopithecines* specimens were fed hard items, such as meat, mature or fibrous leaves, or pithy fruits (Teaford&Ungar 2000). Brockman and Schaik (2005) studies show that the microwear striations and pitting on incisors in savanna habitat (vegetation) are contributed to the early hominid' diets, while Grine (1981) suggested striations on molars and indicate corrosive vegetation. Striations and pitting rate are also related to tooth wear as well as quality of habitat. For instance, when both the foods arising from height upon the land and those close to the soil are compared, the former is better than the latter, as they do not often result in tooth wear like the latter. Also, grazing close to the soil would cause eating of more grit, when compared with getting food from tall trees. This result shows the early hominin' diet, which is comprised from some grit or dust surrounded foods (Brockman and Schaik, 2005). Consequently, it is possible that they were moving their foods from the bushes area or shrubs closer area to the land because of the environment/ climate changes. On the other hand, when compared to early species, *Australopithecus anamensis* is defined as occupying dry, possibly open, wooded or bush-land habitats in the riverine forest (Leakey et al., 1995, White et al., 2006). It contains open habitat foods, such as, grass, seeds, sedges, etc., as well as fruits and roots. The diet of *Astralopithecus anamensis* was exactly abrasive and plenty in seeds, leaves and corms, like today's

primate. They fed on different kinds of fruits, but in smaller proportions than *Australopithecus afarensis*. Nevertheless, the diet of *Au. anamensis* and *Au. afarensis* is discussed because of the changing of the dietary habits from soft, sugary forest fruits (closed area) to brittle and hard or abrasive items (open area) (Ward et al., 1999; Teaford&Ungar, 2000; White et al., 2000; Wood&Richmond, 2000; Walker, 2002).

The habitat of *Australopithecus afarensis* from Laetoli and Hadar is dry and open savannah (Bonnefille and Riollet, 1987), but faunal evidence shows wooded habitats (Andrews, 1989). Hadar formation is comprised of complex structure, including riverine forests, woodlands wet/dry grassland with bush and grass location (Gray, 1980). This vegetation is changed together with climatic changes. However, some evidence shows that *Australopithecus afarensis* would prefer drier more open habitats (Eck and Reed, 1996). Their diet consists of fruits of forest, hard and corrosive foods. In a similar way, *Australopithecus afarensis* was addicted to the forest fruits, but seasonally sought food in more open settings with 'tougher items including abrasive items' and 'nuts preserved by skins or a hard shell'. Ungar & Teaford (2001) called this a 'mixed forest-savanna source adaptation. In addition, Ungar (2004) suggested that the rate of differences in the occlusal incline and relief in both *Australopithecus afarensis* and chimps is as anticipated to the differences in fallback food items. This refers to the fact that the earliest hominids may have rather soft, sugar-rich fruits instead of hard foods.

Then, *Australopithecus africanus* inhabited closed wooded, bushland and edaphic grassland habitats. Raymond Dart (1925) (Taung specimens) said that the diet or habitat ecology of *Au. africanus* is complex and conflicting. In addition, although, Robinson (1954) stated that *Au. africanus* was an omnivore (Sterkfontein), tooth microscopic studies show that *Au. africanus'* diet shape was fruit and leafs (Grine, 1981; Grine and Kay, 1988, Lacruz et. al., 2005). On the other side, the habitat of the Sterkfontein demonstrates that the habitat in the enclosed of the cave was a woodland riverine ecology enclosed by grassland. There was also a moist natural condition (also tropical elements) (Bamford, 1999) in between 3-2.6 Ma, then, climatic shifts happened in this period. Hence, a new season was dry and open grassland. Isotopic studies are also support that the diet of *Au. africanus* was a combined structure, that is to say, the habitat of *Au. africanus* was comprised of different food items and more multiple than Swartkrans and Tanzania. The first isotopic study (1989) on the Sterkfontein hominins indicates that their habitat was comprised from C_4 items with many of the grazing animals. In other words, *Australopithecus africanus'* diet contains C_4 items, such as, grass, seeds, blades, particularly seeds and root-stocks; C_4 reeds, termites and grazing mammals (Scott et. al., 2005).

The environment choices of *Paranthropus* are poorly known. However, hominid localities reflect more arid and open habitat (in riverine forest area) in Turkana, Kenya. According to the paleoecological studies, the natural living

conditions of *Paranthropus* were drier or drought regions than *Australopithecus africanus* (Vrba, 1975; Grine, 1981). Even though *Paranthropus* was lived in mosaic habitats, the overall dryer factors and possibly longer dry seasons would have decreased the standard and the amount of existing food sources. In the meantime, the Africa Region is characterized by dry and drought environment in dry seasons and a plenty of fibrous plant food, which is relatively hard and tough items. In the same way, Grine (1981) said that *Paranthropus'* diet was rich in the amount of grit, which they preferred in their diets, and which was related with river margins and the edaphic grasslands. *Paranthropus* could not exist in early middle Pleistocene by observers. It was fossilized in arid grassland. This referred to the fact that as the setting had started to be increasingly dry and open during the early Pleistocene, *Paranthropus* probably faced shifting and a reduction of resources. As it is shown here, there is much argument about *Paranthropus'* habitat. For example, according to a stable isotopes analysis, there was a dramatic increase of the amount of the C_3 and C_4 vegetation in Kenya and Olduvai region in Tanzania about 1.7 Ma (Cerling, 1992). In addition, the pollen record indicated that East African localities were covered with arid vegetation 1.8 million years ago (Bonnefille, 1995). Even though the issues of environmental shift and habitat choice are central to questions of early hominid paleoecology and adaptation, there is still unknown in detail relation in between climatic changes in Africa and the habitat of hominids. Also, the diet

of *Paranthropus boisei* is controversial in recent times. Even though, tooth morphology of *Paranthropus boisei* shows that they ate very hard (strong) and abrasive items, such as, seeds and nuts or on roots and tubers, molar microwear studies on *Paranthropus boisei* indicate that their diet or habitat ecology is separate from *Paranthropus robustus* because of feeding on tough and corrosive items. They typically ate hard food items, but in other words, their diet rarely consisted of soft items, like C_4 flora, as against *Paranthropus robustus* in southern Africa. Similarly, the isotopes studies on *Paranthropus boisei* demonstrate that they are fundamentally differentiate from many hominoids (Ungar et. al. 2008). In other words, their diet was variable from C_3, like chimps and gorillas to C_4 like *Au. africanus* and *Paranthropus robustus*. Also, Grine (1986) noted that *Paranthropus'* diet structure was herbivore and verified by its larger premolar and molars and comparatively smaller front teeth. On the other side, Turkana had an arid forest or bush savanna. Hence, reeds were important hominid resources because there was a considerable rise in the number of reeds and grass in the riverine forest region. Finally, the diet of *Paranthropus robustus* is herbivore, which ate just plants, so they adapted to dry/arid habitat (savannah) and open forest area. Then, they had huge post-canine so *Paranthropus robustus* could consume tough and abrasive plant roots, grains and granulates kind of food items (Scott et. al., 2005; Sponheimer et.al., 2006).

1.2. Environmental and Climatic Changes in the Pliocene Period

It has been known that most of the evolution of the Hominidae occurred in the ground of the African Pliocene. The Pliocene is regarded as a period of climatic changes, a transition period from the warm Miocene period to the ice ages of the Pleistocene. The African continent has been affected by the glacial factors in the last ten years, and so it resulted in drier and more open environment (Crowley&North 1991). According to the paleontological and paleobotanical records, there were warm and hazy natural conditions in the Miocene and early Pliocene period in Africa and Africa covered with forest and temporal woodland before this time and also higher rainfall was seen (Bonnefille, 1995). However, together with changing of climatic factors, more open areas were started to see in Africa. Even though there was a precise climatic change in Pliocene, the environmental shift to cooler drier and seasonal factors in Africa was poorly understood. Some researchers (Behrensmeyer et al. 1997) suggest that the environmental change occurred gradually 3 to 2 million years ago. However, others suggested that the significant environmental/climatic shift in the African Plio-Pleistocene took place 2 million years ago (Feibel et al. 1991; Reed, 1997).

On the other hand, Africa was primarily vegetated by C_3 items, most likely shrubland and forest, and no proof of open C_4 grasslands was found, and which are significant today and around 8 million years ago (Cerling, 1992, Cerling et al. 1997).

Globally, the C_3 ecosystems first reprocessed in the tropics and later at the mid-latitudes, with C_4 grasses becoming significant in local ecosystem between 8 and 3 million years ago. Open grasslands appeared later in Africa, between 3 and 2 million years ago, depending on location.

In the Pliocene epoch, there were two most important global climate events: northern hemisphere glaciations (NHG) and a change in the dominant epoch of climate oscillation, both of which happened 2.80 to 2.75 million years ago. The northern hemisphere glaciations occurred before the early Pliocene warm period (EPW), approximately 5.3 to 3.3 million years ago (Ravelo et al., 2004). In early Pliocene period in Africa, there were more humid and warmer climate conditions (the previous 5 Ma). Warm temperature and high rainfall are seen from 5.4 to 3 million years ago (Marlow et al. 2000). Another glacial-force cooling trend began 3.2 Ma and maintained during 2.2 Ma, represented via lower sea surface temperature (SST). Therefore, the amount of mean annual rainfall (MAR) and terrestrial temperatures were gradually decreased within the same time. This factor led the aolian dust levels to increase, so showing xerification by 2.8 million years ago (Bobe et al. 2002). According to sea surface temperature, sea and land temperatures are decreased rapidly (cooling) from 2.1 to 1.9 million years ago. When the temperatures, the aolian dust levels and rainfall returned to pre-1.8 million years ago values, climates remained heavily barren until 1.6 Ma. (Bobe et al. 2002). Another climate transition was realized from 1.0

Ma through 650 Ka, highly reduced sea surface temperature and also drought in tropical Africa (Brockman and Schaik, 2005). Hominin transition started to other localities at 1.8 million years ago and those transition latitudes beyond the subtropics experienced significantly separate climatic models. Ancient temperature climates in latitudes for hominin sites are between 30 and 60 today, cold climates are similar north of 60 latitude today.

When compared with seasonality, the climate is affected via latitude and is relatively specified, which in turn influences the habitat/diet type of species. It has been seen that while low latitude forest environments (habitat) had short arid (dry) seasons and long wet seasons, open woodlands at the same latitudes experienced longer dry seasons and shorter wet ones. The lengths of dry and wet seasons or strength of winter are affected by local and regional factors.

1.2.1. The Environmental Effect on the Early Hominids' Diet

The glacial period caused climatic and environmental (changing habitat) changes, so source availability is affected (Reed & Fish, 2005). Also, seasonal differences are affected by climatic changes in long duration. Variances in the amount of dry seasons especially caused major levels of foraging force for early specimens. Together with the rise of dry season in 3.0 and 2.5 Ma, using source is affected, considerably. In the meantime, while some early *Australopithecus* and *Paranthropus* specimens were

feeding on USO (underground storage organ), other populations were based on animal sources. Also, the climate change process (in particular ocean-atmosphere-soil connections) is associated with the human and faunal evolution in Africa. Especially, geo- and biochemical data and climate factors that have indicated that the African drought is checked via the tropical sea surface temperature, that east African drought starting about 3 million years ago was likely checked by the Indian Ocean SST (sea surface temperature), and that motional diversifying in C_3 and C_4 items has been controlled by shifts in monsoonal precipitation driven by low-latitude insolation shifts (Schefub et al., 2003). These findings indicated that the east African climate shift has largely been ruled via the ocean-atmosphere line in the low latitudes so affected Pliocene hominins and their habitats. In other respects, According to Potts (2007), during the Pliocene period, the hominin evolution was primarily based on three interrelated factors: mobility, foraging and diet. Generally, organisms are responded to environmental and climatic changes by mobility, foraging and dietary ecology, in particular by tracking favored sources or climatic requirements, by shifting the amount of time and strategy of finding food, and changing to alternative foods when necessary. These three factors were certainly influenced by environmental and climatic conditions. Therefore, researches that aim at linking the Pliocene faunal record to hominin adaptive shift may profit by also focusing on the evidence of altering models of locomotors, foraging and diet in other large mammals.

The transition became at different proportions and with separate timing depending on sites, although the general leaning in Africa was on more open dry habitats from 3 to 1.0 million years ago. For instance, a species behavior and environmental shift in the Omo, 2.8 million years ago, whereas a habitat change occurred slightly earlier at the Hadar sites 3.18 to 2.95 million years ago (Reed 1997; Bobe and Eck 2001). Behrensmeyer et al. (1997) supported that the gradual species turnover reflects the environment shift across this whole of time in West Turkana. 1.7 million years ago, the habitat of hominins (outside of the subtropics) was warm temporary woodlands and grasslands or tundra. This temporary forest with several trees supplying fruits and nuts would have existed in some interglacial cycles. Natural habitat of the hominins was surrounded with the Mediterranean Sea throughout the Pleistocene period and its climate conditions were warmer than the north.

On the other hand, according to ecological proof from early hominin localities, the characteristics of early species' diet were suitable for living in different natural habitats; that is to say, they could feed on different food items. In general, the formation of food items is enlarged in the long rainy seasons every year. Nevertheless, there were arid natural conditions, so the generation of flowers, fruits and flush leaves was decreased. There was a dramatic decrease in primary prolificacy and sources were difficult to find in the arid natural conditions, due to the global climatic changes, dated 3.2 million years ago (Marlow et al. 2000). There was also a gradual decrease in the quantity of upon-land plant items existing for hominid exploitation. The

longer periods of aridity influenced food items, like plants, but in such situations—if temporary—they fed on store energy in underground storage organs, rather than leaves or fruits. Consequently, rhizomes and bulbs would be present during most of the arid period and supply the requirement diet to the early hominids. For example, these results for *Australopithecus afarensis* and the early hominids, such that a shift to longer arid periods began by raised drought (Vrba, 1995; Behrensmeyer et al., 1997; Bobe and Eck, 2001) could have pushed the species toward extinction. During the long dry periods, some early *Australopithecus* specimens may have changed their foraging attempt to underground storage organs, and within time *Paranthropus* specimens improved. Other early hominid species shifted to critical sources in response to extending arid periods, via combining marrow or meat into their diet ecology, included through the use of stone tools.

Biological evolution and natural conditions are parallel to each other, and they consist of small and large shifts in the earth **(**especially in habitat from rainy to arid due to environmental changes). These changes on climate and environment affect and influence the Plio-Pleistocene hominids, directly. It is also a part of evolutionary changes. The evolution of mammals, as well as early specimens in Africa is also related to the continental climate that is gradually becoming cold and arid. This took part in the savannah, rather than the forested areas. Together with increasing the bushland and grassland, there was a considerably decrease of the amount of forested regions. Then, early

specimens were adapted to increased thermoregulatory stress and moved to the terrestrial and more open habitats (Bromage and Schrenk, 1999). Vrba (1995) also supported that climatic alteration played significant role in this theory.

1.3. Early Hominids' Tooth Morphology

Tooth morphology is one of the most important points to understand the behavioral and ecological differences among early specimens on habitat/diet. In recent years, most researchers have been focusing on the Pliocene period hominin teeth, in regard to diet. The finding of new fossils from early Pliocene has posed important questions about the role of the dietary shifts in the early hominins teeth (White et al. 1994). According to Teaford and Ungar (2000), both *Ardipithecus* and *Australopithecus* were first half of human evolution and significant shifts occurred in their diet/habitat in these periods (4.4-2.2 Ma). Together with that, the dietary/habitat change in *Australopithecines* is probably parallel with the climatic and environmental changes. While the early hominids were living in forested areas (Vrba, 1985, 1988), together with important climatic and environmental changes, these were surrounded with open savannah (Dart, 1925). We can understand these environmental shifts from their tooth morphology i.e. tooth size and shape, enamel thickness, dental microwear and mandibular corpus size and shape.

According to Jolly (1970), when the incisors and molars of *Australopithecus* are compared, the incisors of *Australopithecus*

are small in size, thus it is likely to be associated with terrestrial seed-feeding. Even though this opinion can be problematic (Dunbar 1976), Jolly's studies have revived a remarkable study on the early hominin dietary adaptations with relative 'incisor size' (associated with different dietary regimens), in a broad variety of fossil and living primates. For instance, the relationship between the incisor row length and body size on the living anthropoids is investigated. According to this inferred result, if specimens consumed larger food items and tougher fruits, their incisive size would be typically larger, and similarly, if specimens consumed smaller food items, like berries and leaves, their incisive size would be small (Hylander 1975). Many researchers like Jolly (1970) and Hylander (1975), focused on the incisor size in early hominids to understand their diet.

On the other hand, thanks to the incisor size, as it can reveal significant details on the diet and the use of teeth in the early *Australopithecines*, as well as estimate the species body weight (Jungers 1988; McHenry 1992). In general, *Australopithecines'* incisor sizes are considerably similar, like gorilla. Even though they used these teeth less than both the orangutan and chimpanzee, *Australopithecines* used their incisors in the same way in nutrition (Kay 1984; Ungar, 2011). This database provides some idea about the foods eaten and the required incisor-based preparation. For example, gibbons do not have as large incisors as the orangutans, so they fed on smaller fruits, needing little incisor-based preparation (Ungar, 2011). According to this idea, *Australopithecines* had probably put

less force on foods that needed major incisor use, such as those with thick husks and flesh adherent to large and hard seeds. *Australopithecus* specimens also have large and flat molars (Robinson 1956). When gracile *Australopithecus* is compared with robust *Australopithecus*, in regard to the occlusal relief, there are definitely significant differences between them (Grine 1981). Nevertheless, when compared with other primates, *Australopithecus'* molars are still large and flat. Moreover, the earliest hominids' teeth are larger than those of the modern orangutans aspect from the post-canine tooth area. As it can be expected, the Miocene hominoids indicate a major variety of mandibular molar sizes. Many post-canine areas (mesiodistal & buccolingual diameters) are larger than *Ardipithecus* and *Au. anamensis* areas. For example, *Ouranopithecus* has larger post-canine area than *Au. anamensis*. The post-canine tooth area provided that the earliest hominids get a good improvement leading into the hominids that appeared later, but that their post-canine tooth area is smaller than those hominoids from the Miocene period.

There is no doubt that some foods features of early specimens were changing throughout the evolutionary process and this change are affected the tooth size. Lucas et al. (1986) also stated that the meaning of this alteration in tooth size is adapting the changing food traits, such as their shape, size and corrosiveness. For example, their molars and premolars were getting larger and larger. Nevertheless, the tooth size in the Miocene period indicates that it cannot

identify the specific point in which the primary change to a hominid diet occurred.

On the other hand, the post-canine tooth size (M1 and M3 areas) demonstrates that this proportion is associated with the consumption of flowers, fruits and leaves in dietary habits. In other words, anthropoids have a high rate of M1 to M3 area due to consuming more fruit than others (with a high rate of M1 to M3 area) (Lucas et al. 1986). There is a difference in this ratio, between the earliest hominids and Miocene apes. For instance, *Ardipithecus* has higher ratios of M1-M3 areas than Miocene apes. It might be deduced that the earliest hominids used to consume more fruits in their diet or not, according to the tooth shape, which should be analyzed.

The alteration of 'tooth shape' is adaptive to the changes in the features of foods, such as hardness, toughness and deformability (Lucas et al. 1986, 1994).There is no doubt that foods are complex-structured, so it is not possible to define the whole of the internal features and reflect to hominids' teeth, but the capacity of many teeth can be learned. For instance, it is difficult to break tough foods, so generally foods are cut between the leading sides of the sharp crests. In contrast, it is easy to break hard brittle items, but difficult to penetrate, so generally foods are crushed between the planar surfaces. Also, crested teeth split tough food (leaves), while flatter and rounder teeth are more adapted to fruit-eater diet. According to Kay (1984), more leaf, fruit-eater species have the longest cutting ratios, succeeding brittle and soft fruits,

like *Ardipithecus*, while strong-object eaters have the shortest cutting crests, like *Australopithecus* and *Paranthropus*. This situation is also controlled by certain environmental factors. Fruit-leaves eaters are affected in forest areas, while strong-object eaters (grazing) are affected in grassland and open woodlands (*figure 2*).

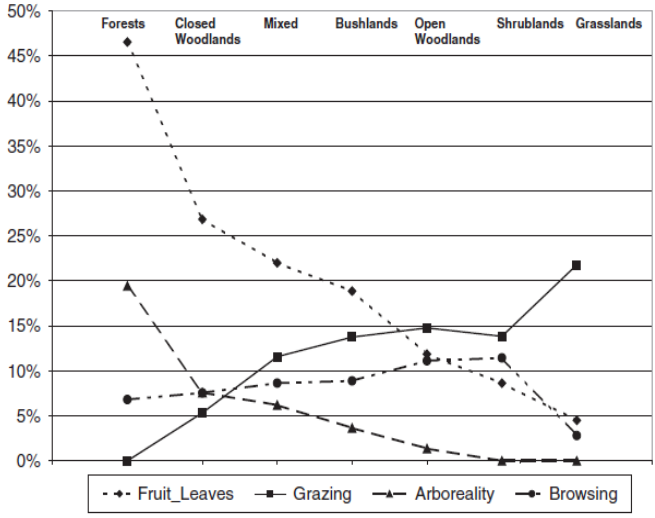

Figure 2. *Frugivory, Grazing, Arboreality and Browsing in the African Habitat (from fig.17.2, p. 502, Reed & Fish, 2005).*

Together with climatic changes, the habitats of the early hominids are changed from forested to grasslands areas (*figure 2*). That is why their diet was affected. For example, there is a dramatic decrease of fruit and leaves from forested areas to the savannah. According to this result (*figure 2*), *Ardipithecus ramidus* have the longest cutting crest.

The cutting crest researches on early hominids indicate that the occlusal relief of *Paranthropus robustus* was smaller in rate than *Australopithecus africanus* because of the dietary (habitat) differences (environmental changes) between them (Grine 1981). Also, the molar teeth of *Australopithecines* are blunt and flat and some extant hominoids lacked the high cutting crests (Kay 1985). From this perspective, the early hominins would have had difficulty fracture down tough, flexible food items, such as veins, stems of leaves and soft seed coats, even though they likely were talented at processing flowers and buds.

On the other hand, Lucas and Peters (2000) suggest that early species did not eat meat, that is, their dentitions were not adapted to feeding on meat, and so their teeth were not sharp. On the contrary, their teeth were blunt and flat-structured, so they were adapted to fracture hard brittle foods. However, how about these soft fruits? It is related to the toughness of fruits. If species eat tough items, they would also require retaining and slicing among the teeth, so early specimens would be totally unaffected by it. Consequently, according to tooth shape, the Miocene apes had variety adaptations, containing soft fruit feeding, folivory, and hard food eating. This variety is also seen in living and, particularly the early hominids. All evidence shows that when *Australopithecines'* molars are compared to living and fossil apes, *Australopithecines* had flat molars. These teeth were well suited for cutting brittle, hard food items, involving some fruits and nut, and, soft weak items, such as buds and flowers, but they were not breaking down tough pliant

items, like soft seed pods. Investigators focused on tooth shape because the alterations in tooth shape are a means of adapting to the shifts in the internal features of food items, such as, their hardness, force and deformability. Also, primates' incisors and molars (microscopic wear) reflect the usage of tooth and the type of diet, but the microwear studies of early *Australopithecus* offer little information about the diet.

Another interesting point is the 'enamel thicknesses' about diet. What is the reason of the differences of enamel thickness? It seems that there is a correlation between the consumption of soft and hard foods, or abrasive food, and how thick a molar's enamel is (Kay 1981). It is also affected by many factors (Macho & Thackeray 1992; Macho &Berner 1993), so there is no surprise that there is an obvious relationship between diet and enamel. Furthermore, the enamel thickness by itself does not necessarily supply preservation toward hard foods, which generally cause the breaking of enamel (Teaford et al. 1996). The best preservation against this is prism or crystallite decussation or interweaving. When the early specimens' enamel thickness was examined, although there are some differences as methodological, it appears that *Australopithecus* and *Paranthropus'* enamel were thick (*figure 3)*, when compared to other primates' (Robinson 1956; Kay 1985; Beynon& Wood 1987; Grine& Martin 1988; Macho & Thackeray 1992). This view might be changing, when new taxa is found. For example, *Otavipithecus* had a thin enamel shape, like *Ardipithecus* (White et al. 1994) (*figure 3*).

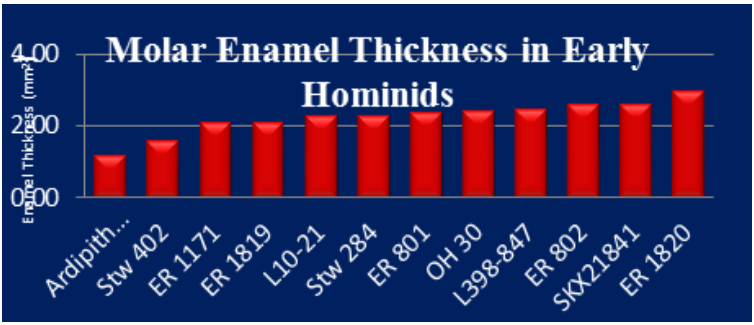

Figure 3. *Molar Thickness in Early Hominids (data from Beynon and Wood, 1987; Grine and Martin, 1988; White et al., 1994).*

One of the most common things found within the hominid fossil localities is the mandibular pieces and this bone has been adapted to withstand emphasis and strains, relating to oral food processing. This structure provides some information about diet, so it focused on the 'mandibular corpus size and shape'. When compared with extant hominids, the corpus of *Australopithecus afarensis* and *africanus* is thick (Daegling&Grine 1991). The same situation is seen in *Paranthropus boisei* and robustus. However, the mandibular corpus size of *Paranthropus* is higher than *Australopithecus* specimens (*figure 4*). This situation might be explaining both functional and nonfunctional affects. For instance, large or huge cheek teeth are identified by a thick mandibular corpus or a decreased canine size. That is not sufficient clarification; however, as *Australopithecus* has wide mandibles when compared to the molar size, and there seems to be no connection between the mandibular robustness and the canine size within *Australopithecines* (Daegling&Grine 1991).

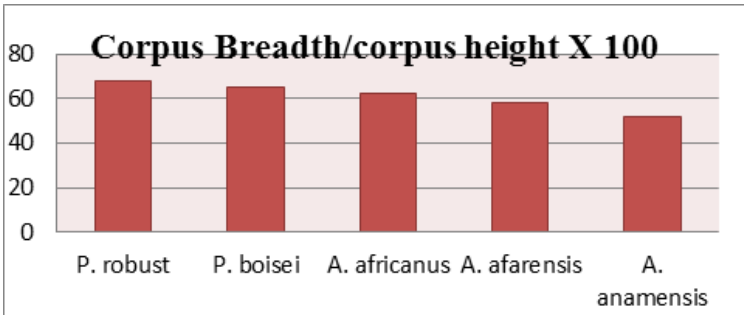

Figure 4. *Measurement of Mandibular Shape of Early Hominids (data from refs. 75-76, and 85 and M. Leakey)*

It is evident that the mandibular corpus of *Australopithecus* associates with the functional demands of mastication. Thickened mandibles can act to resist extreme emphasis relating to the transverse inclination (wishbone) and torsion. Because this bone emphasis decreases toward the back of the corpus, torsion is probably more significant clarification. Corpus torsion can arise from bite force and muscle action throughout mastication. Hence, the mandibular structure of *Australopithecines* provides elevated stresses, relating to the unusual mechanical demands. According to Daegling and Grine (1991), *Australopithecines* could be fed fibrous and rough foods, requiring repetitive loadings. The corpus shape of *Ardipithecus ramidus* and *Australopithecus anamensis* gives us information about the differences of the mandibular corpus shape in great apes and later *Australopithecines*. For instance, *Australopithecus anamensis'* measure is 53.5 below M1 and these values decrease in extant hominoids, like Pan's

measure is 39.2-57.8, gorilla is 43.5-59.7 (Daegling and Grine 1991; Lockwood et al. 2000). Consequently, according to the mandibular corpus structure, there are differences between the gracile *Australopithecines* and living apes. These differences arise from their habitat (after climatic/environmental change).

To sum up, when *Australopithecus* specimens are compared with the Miocene apes, *Australopithecines* have a complex morphological structure about diet. These early specimens have small/middle incisor sized, large and flat molars, thick enamel shape and mandibular corpus. This situation arises from dietary/habitat changes (affected by environmental changes) between them. *Australopithecines'* thick enamel shape and flat molars indicate that they did not fracture tough items, so they were not adapted for feeding on tough fruits, leaves or meat. It is also supported by a microwear analysis. Instead, *Australopithecines* were capable of eating hard and brittle food items. Their large/flat molars were suitable for crushing, and their thick enamel also withstood wearing and fracture. In addition, their mandibular corpus had high occlusal relief, so they had an advantage for resisting failure. In general, the early hominids could feed on both abrasive and nonabrasive food items. Therefore, they adapted in a variety of habitats, ranging from forest to open savannah.

1.3.1. Dental Microwear of Early Species

Since the early 1980s, dental microwear studies have been continued and these studies are associated with dietary habits of extinct hominid specimens (e.g., Grine, 1981 and 1986;

Walker, 1981; Grine and Kay, 1988; Scott et al., 2005; Ungar et al., 2008 and 2010). Differences in diet of the early hominids can be defined by microwear studies, enabling the observation of seasonal and natural differences, like ecologic (Teaford and Oyen, 1989; Teaford and Robinson, 1989; Teaford and Glander, 1996: Teaford and Runestad, 1992). Microwear studies in diet ecology may represent subtle, short-term alteration, and reflect the specific seasons and climatic conditions.

The displayable connection between microwear studies and diet is like a relationship between the enamel thickness and the features of the food items. That connection shows especially the occlusal mechanics, where the angle of approach between opposing teeth is directed, if not dictated by the fracture quantity of food. Sometimes, it is a misunderstanding that food pieces are either too soft or too big to have led to tooth abrasion, which is the notion that the food item's shape, size and orientation based on in large measure on whether the corrosives are engraved through a surface (led to striated in line with horizontal slip), or stressed into the enamel with force directed normal to that surface (led to pitting). Consequently, hard or brittle foods (nuts, bones) caused wear, like pits because these abrasive items are stressed into the enamel, as teeth approach one another with forces normal to the occlusal plane, while tough items (leaves or meat) led to scratches, as the abrasives are dragged through the occlusal surface, as opposing teeth shear past one another (Ungar, 2010). Also, exogenous grit (Nystrom et al., 2004), surface fractal complexity or shift in apparent roughness and

anisotropy is affected in the generation of dental microwear. Because of large complexity and anisotropy values, it consisted of serious pitting and highly in-line striations (*figure 5*).

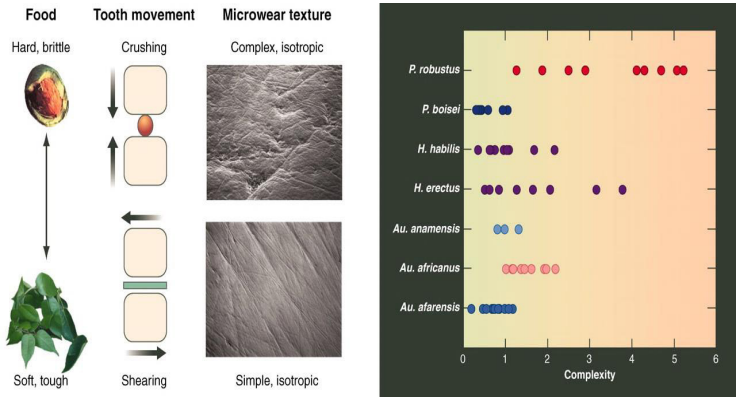

Figure 5. *Microwear Studies of Early Hominids (from Fig 2, Scott, 2005; Ungar et al., 2011).*

Microwear studies on *Australopithecines* are little known. When molar microwear is observed in *Ardipithecus ramidus*, their molars do not demonstrate the feeding of hard or brittle items in their dietary habits. Then, according to SEM-derived occlusal microwear data on the dietary habits of *Australopithecus anamensis*, the diet and microwear pattern of gorillas and chimpanzees is reference to diet and microwear pattern of *Australopithecus anamensis*, that is to say, their diet is almost the same, such as, soft and thin food items. Also, microwear studies do not support feeding with hard and brittle food items (Grine et al., 2006). Even though, the craniodental construction of *Au. anamensis* displayed consumption of hard and brittle

items, the microwear analysis demonstrated consumption of soft food items. Next, when the occlusal microwear analysis data on *Australopithecus afarensis* was observed, it encountered surprising results. Gorillas and *theropithecus* are the best modern analogs for the dietary choice in those *Australopithecus afarensis* samples (Grine et al., 2006; Ungar et al., 2010). Researchers focused on front teeth of *Australopithecus afarensis*, suggesting that they survived in savannah sources. Moreover, *Au. afarensis* had a mosaic structure. For instance, their fine wear scratch is like a gorilla, whereas their pits and microflakes are like a baboon. They also use incisors to peel sanded plants pieces, like roots, seeds and rhizomes. On the other hand, although *Au. afarensis'* diet is a wide variety of food items, containing hard and brittle food items, such as, seeds, nuts and hard fruits (Wood and Richmond, 2000: 29), their molars' microwear suggests that *Au. afarensis* did not always eat hard items (not dominated hard foods). Microwear studies about *Australopithecus africanus* molars have shown dominant surfaces with anisotropicall oriented small pits and striae (Grine, 1986; Grine and Kay, 1988). The average width of wear striae in *Au. africanus* is the same as *Australopithecus afarensis*, also the scratches are narrower and longer and they indicate more homogeneity in direction. The rate of pits is nearly the same in both of them. However, the pits tend to be larger in *Au. africanus* because of the quality of foods. There was a great difficulty in *Au. africanus* about the dietary, when compared to *Au. afarensis*. Although, the microwear complexity of *Au.*

africanus is higher in degree (i.e., pitting) than *Au. afarensis* and *Paranthropus* specimens, it is not as higher as *Cercocebus* (hard-food items consumer). In addition, when *Au. africanus'* anterior teeth are compared with *Paranthropus*, their teeth show the consumption of a great variety of foods (containing larger and more abrasive). On the contrary, *Au. africanus'* premolars were adapted to open hard items, while their molars were adapted to soft seeds (Strait et al., 2009). Also, when compared to *Paranthropus*, *Au. africanus* fed on more soft fruits and leaves (Teaford 1988).The microwear analysis indicates that *Paranthropus robustus* diet is dissimilar to the diet of *Au. africanus*. These differences are not just in the size of food items, but are also related to the standard of the foods masticated. For instance, it consisted of higher percentage and larger pits in *Paranthropus robustus*, 49% compared to *Au. africanus* 31% and *afarensis* 29% (Scott et al., 2005) because of hard object eaters.

When the complexity and anisotropy rate of *Paranthropus robustus* is compared to other hominins, it has the maximum complexity rate and minimum anisotropy rate (Scott, 2005). Also, the microwear analysis shows feeding on very hard and brittle objects of *Paranthropus*. The first microwear analysis (SEM analysis) on *Paranthropus boisei* demonstrates that *Paranthropus boisei'*s diet may have required elongated feeding on tough or fibrous food items, perhaps with comparatively small dietary worth, instead of the consumption of hard items (Walker, 1981). After thirty

years, Ungar et al., (2008) undertook a microwear analysis on *Paranthropus boisei* and this revealed a surprising result. That research is that *Paranthropus boisei* do not have large and heavy pits as expected (hard food items), unlike fine scratches that are present on *Paranthropus boisei'*s tooth morphology. This situation (parallel and big scratches) has been seen also in tough items grazers. The microwear shape complexity of *Paranthropus boisei* is low, while their anisotropy values are moderate. This dietary habit is similar to *Au. anamensis* and *Au. afarensis* (referring to food items with fracture features) (Ungar et al., 2008; Ungar et al. 2010). Also, *Paranthropus boisei'*s wear structure is considerably different from *Paranthropus robustus* because of dissimilar dietary habits and foraging tactics of them. *Paranthropus robustus'* abrasion shape is linked to many hard item eaters like *Lophocebusalbigena*, while *Paranthropus boisei'*s diet is associated with the extant African apes. Eating hard food items has not been seen in microwear data, and its microwear analysis is seen to suppose very specific dietary habit than *Paranthropus robustus*. However, Suwa et al., (2009) suggest that *Paranthropus boisei'* diet occurred from abrasive and hard items, so they have major and powerful masticatory system

1.3.2. Definition of Stable Isotopic Analysis

The stable isotopes analysis has provided relative rate of plants, using the C_3 (trees, bushes, forbs) or C_4 (tropical grasses and some sedges) food for early hominin. This is one of the most

important points in early hominin diet studies (Lee-Thorp and Sponheimer, 2006). There are two major points in this analysis, which are nitrogen isotope $^{15}N/^{14}N$ (composition of bone) and carbon isotope $^{13}C/^{12}C$ (formation of tooth enamel). The identification of the carbon isotope formation of enamel is associated with oxygen isotope ($^{18}O/^{16}O$) formation (ecological and climatic information are ensured by it). Another important point is nitrogen isotopes. It has provided the learning of nutritious elements, particularly when the diet contains meat in drought environments. However, the finding of hard tissue is limited, because it needs to have the maximum protection limit of some 200 kya, even under perfect circumstances. It is restricted to more recent hominin specimens. Even though Australopithecus pieces do not contain collagen, it can be computed from their skeletons by oxygen and carbon isotope analysis.

Stable carbon isotopes studies might be one of the most considerably used and perhaps well-understood of the biogeochemical researches for paleo-dietary reconstruction. This point is associated with the variances of plants, which included different photosynthetic path (and and crassulacean acid metabolism). In addition, in comparison to plants (present in subtropical areas and contain grasses and reeds in temperate areas, and a limited number of dry or sline-adapted shrubs), those that employ the plants (consisted of whole trees, shrubs, temperate environmental conditions and bush land) are heavily extinct in ^{13}C proportional to atmospheric CO_2. Therefore, plants are clearly higher in the $\delta^{13}C$ values than the plants.

Environmental factors are emphasized in heavy forest area, which included items, so it caused lower $\delta^{13}C$ values (van der Merwe and Medina, 1989), unlike dry and drought seasons which resulted in higher $\delta^{13}C$ values. Therefore, C_4 items were seen in *Australopithecus* and *Paranthropus'* habitats. For Ardipithecus ramidus **(**in the Aramis region and Duma) Carbon isotope combination in Aramis display C_4 biomass ratio is bigger than 40%, that is to say, tree-bush savannah, dry-bush savannah and open savannah flora is dominant, rather than forested canopy of 5-25%. It is covered with arid shrub savannah, tree bush savannah, bush savannah, edaphic grassland or open savannah kinds of vegetation (Cerling et al., 2010). Moreover, the carbon isotope from bovid tooth enamel is offered by White et al, (2009) and examined the environment conditions (from woodland to savannah) (Cerling et. al., 2010). Therefore, for Aramis, it can be stated that there was open savannah grassland, as well as riparian woodland and forests areas (Cerling et al., 2010). On the other hand, the dental morphology of *Ardipithecus ramidus* shows that it was both 'omnivory' and 'fruit-eater' (Suwa et al., 2009). Particularly, in the reconstruction of early hominin diets, it is observed, in tropical African environments, that almost all trees, bushes and forbs used , whereas grasses and sedges utilized the pathway. Then, these different plants are incorporated with each other, with the result that plants consumers have very separate than eat plants (Lee-Thorp and van der Merwe, 1987).

Both the microwear analysis and the carbon isotope analysis provided surprising results about *Paranthropus* diet. Firstly, it has been seen that the environmental and geographical factors greatly affected *Australopithecus* diet; in both Eastern African *Paranthropus* and *Australopithecus*, the complexity rate on microwear texture is not as higher as their South African congeners. In a similar way, the carbon isotope components of *Paranthropus robustus* and *Paranthropus boisei* are different with each other. C_3 plants fracture rate is higher in the South African robust *Australopithecines*. Secondly, the diet of *Paranthropus robustus* is not merely herbivorous. However, when Sr/Ca data on *Paranthropus robustus* is observed, this was not also supported omnivory in *Paranthropus robustus*, that is, *Paranthropus robustus* and *Paranthropus boisei* did not have one type of diet, including C_3 and C_4 (heavily). The carbon isotope values of *Paranthropus robustus* supported that the diet of *Paranthropus robustus* is comprised of C_4 items about 35-40%. For this reason, although it fed on basically C_3 items, like fruits and nuts, it fed on a significant quantity of C_4 like sedges and grasses.

CHAPTER 2

DATA COLLECTION AND SAMPLES

In this research, the mandibles of *Ardipithecus ramidus*, *Australopithecus anamensis*, *afarensis* and *africanus*, and *Paranthropus boisei* and *robustus* are used as the materials. Important measurements are taken on the premolars and molars of specimens, such as, the mesiodistal crown diameter from P3 to M3, the buccolingual crown diameter from P3 to M3, and the corpus height and width from M1 for compared with each other, and also post-canine area (P3-M3, the product of the mesiodistal and buccolingual diameters) and molar tooth area (M1-M3) are computed from these values. These measurements provide much information about specimens masticatory anatomy, according to habitat and diet. Some of the measurements are collected

from the published, while others are taken by manually with calipers. There are 85 cases categorized by 6 of specimens in this dataset. Primarily, new variables are generated, such as the habitat (forest/closed woodland; open woodland and open woodland, bushland, edaphic grasslands), diet (C3 soft foods and C4 hard foods) etc. These measurements are utilized with statistical analysis to determine the effect of different habitats on different masticatory anatomies.

2.1. Methodology

In this project, four different analyses are used respectively:

- *Descriptive Statistics/ Explore:* in order to show both the distribution of specimens tooth measurements and the distribution in habitat of these variables.
- *Kruskal-Wallis Test:* in order to identify any significant differences among masticatory anatomy values according to specimens, habitat and diet.
- *Anova:* in order to define any statically significant difference between the habitat and diet group means and corpus height and width M1,
- *Principle Components Analysis*: in order to determine the relationship of different masticatory anatomies of specimens.

2.2. Results

As the descriptive statics are examined, it can be seen that *Paranthropus boisei'* variables which are mesiodistal and buccolingual diameter from P3 to M3 are larger values than other specimens, and followed by *Paranthropus robustus*,

Australopithecus africanus and *afarensis*. However, unexpected results have been found in some distribution of specimens tooth measurements. For example, the *anamensis* and *Australopithecus afarensis* are larger than *Australopithecus africanus (figure 6-7)*.

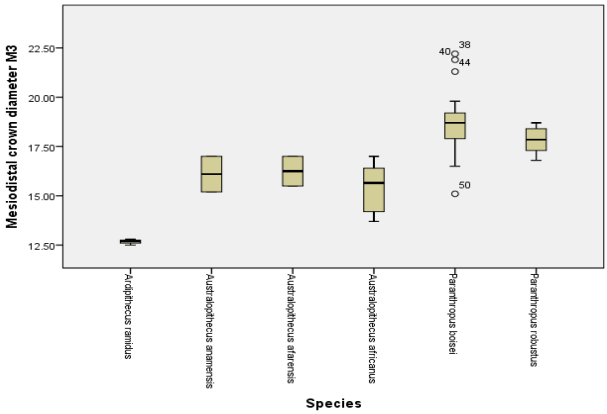

Figure 6. *Distribution of Mesiodistal Crown Diameter M3 on Specimens*

Figure 7. *Distribution of Buccolingual Crown Diameter P3 on Specimens*

The reason is that while some measurements are taken normally (just left or right side from teeth), other measurements are taken from maximum values of tooth measurements (MD-BL from published). Therefore, some variables are different among *Ardipithecus*, *Australopithecus* and *Paranthropus* specimens like these. Of course, it might be missing data of specimens; that is to say, the number of specimens is not equal to each other. On the other hand, as the distribution on habitat of these variables is observed, these variables are in larger values in open woodlands, bushlands and edaphic grasslands followed by open woodlands and forest/closed woodlands. It can be stated that masticatory anatomy is more developed in open woodlands, bushlands and edaphic grasslands than forest/closed woodland. All of masticatory values are positioned in different habitats due to the variety of habitats.

As the Kruskal-Wallis Test results are observed in this project, it can be seen that the Kruskal-Wallis Test is performed to understand whether different tooth characters differed based on test type of habitats, specimens and diet. We can report that firstly, *Paranthropus boisei* is larger in values than other specimens. The mean rank of all of variables (mesiodistal and buccolingual diameter (P3-M3) and corpus height and width M1) for each specimens group can be used to compare the effect of the different specimens. Whether these specimens, habitat and diet groups have different masticatory tooth characters can be assessed using the Test statistics tables which present the result of the Kruskal-Wallis H test.

Table 1. The Test Statistic Table of Masticatory Anatomy on Specimens

Test Statistics[a,b]

	Chi-Square	df	Asymp. Sig.
Mesiodistal crown diameter M1	50.090	5	.000
Mesiodistal crown diameter M2	39.732	5	.000
Mesiodistal crown diameter M3	21.950	5	.001
Mesiodistal crown diameter P3	15.711	5	.008
Mesiodistal crown diameter P4	37.354	5	.000
Buccolingual crown diameter M1	33.869	5	.000
Buccolingual crown diameter M2	39.420	5	.000
Buccolingual crown diameter M3	23.149	5	.000
Buccolingual crown diameter P3	10.367	5	.065
Buccolingual crown diameter P4	32.284	5	.000
Corpus height M1	25.833	5	.000
Corpus width M1	32.516	5	.000
Postcanine tooth are P3-M3	15.321	5	.009
Molar tooth area M1-M3	15.242	5	.009

a) Kruskal-Wallis Test

b) Grouping variable: Specimens

A Kruskal-Wallis test showed that there was a statistically significant difference in masticatory anatomy between the different specimens in the table 1, p = between 0.000 and 0.065, and the mean rank of specimens is shown in table 2. According to this table, Paranthropus boisei is larger in mean rank than other specimens, followed by Paranthropus robustus, Australopithecus africanus. On the other hand, the distribution of masticatory anatomy of specimens is observed in the figure below (8-14):

Table 2. Mean Rank of Masticatory Anatomy Characters of Specimens in the Kruskal-Wallis Test

Ranks

	Species	N	Mean Rank
Mesiodistal crown diameter M1	Ardipithecus ramidus	6	3.50
	Australopithecus anamensis	4	11.88
	Australopithecus afarensis	6	17.58
	Australopithecus africanus	9	20.22
	Paranthropus boisei	28	49.89
	Paranthropus robustus	12	32.67
	Total	65	
Mesiodistal crown diameter M2	Ardipithecus ramidus	5	3.00
	Australopithecus anamensis	5	15.20
	Australopithecus afarensis	5	20.90
	Australopithecus africanus	11	17.86
	Paranthropus boisei	23	43.98
	Paranthropus robustus	10	36.65
	Total	59	
Mesiodistal crown diameter M3	Ardipithecus ramidus	3	2.00
	Australopithecus anamensis	2	12.00
	Australopithecus afarensis	2	12.50
	Australopithecus africanus	6	8.75
	Paranthropus boisei	18	25.83
	Paranthropus robustus	6	21.75
	Total	37	
Mesiodistal crown diameter P3	Ardipithecus ramidus	3	2.00
	Australopithecus anamensis	2	6.75
	Australopithecus afarensis	2	8.50
	Australopithecus africanus	3	11.00
	Paranthropus boisei	10	18.35
	Paranthropus robustus	4	11.75
	Total	24	
Mesiodistal crown diameter P4	Ardipithecus ramidus	4	3.75
	Australopithecus anamensis	5	8.20
	Australopithecus afarensis	4	11.88
	Australopithecus africanus	7	15.57
	Paranthropus boisei	21	35.95
	Paranthropus robustus	6	26.75
	Total	47	
Buccolingual crown diameter M1	Ardipithecus ramidus	6	3.75
	Australopithecus anamensis	4	13.25
	Australopithecus afarensis	4	14.75
	Australopithecus africanus	9	21.50
	Paranthropus boisei	15	39.17
	Paranthropus robustus	11	28.14
	Total	49	
Buccolingual crown diameter M2	Ardipithecus ramidus	5	3.00
	Australopithecus anamensis	4	14.50
	Australopithecus afarensis	5	13.70
	Australopithecus africanus	11	20.14
	Paranthropus boisei	24	42.88
	Paranthropus robustus	9	35.44
	Total	58	
Buccolingual crown diameter M3	Ardipithecus ramidus	3	2.00
	Australopithecus anamensis	2	8.25
	Australopithecus afarensis	2	9.00
	Australopithecus africanus	6	12.50
	Paranthropus boisei	13	22.85
	Paranthropus robustus	3	7.50
	Total	29	
Buccolingual crown diameter P3	Ardipithecus ramidus	3	2.00
	Australopithecus anamensis	3	12.50
	Australopithecus afarensis	2	16.00
	Australopithecus africanus	3	11.17
	Paranthropus boisei	11	17.45
	Paranthropus robustus	4	12.50
	Total	26	
Buccolingual crown diameter P4	Ardipithecus ramidus	4	3.00
	Australopithecus anamensis	6	8.50
	Australopithecus afarensis	3	11.50
	Australopithecus africanus	6	18.08
	Paranthropus boisei	19	33.13
	Paranthropus robustus	7	28.50
	Total	45	
Corpus height M1	Ardipithecus ramidus	1	2.00
	Australopithecus anamensis	1	3.50
	Australopithecus afarensis	8	9.19
	Australopithecus africanus	9	15.17
	Paranthropus boisei	15	30.60
	Paranthropus robustus	6	24.25
	Total	40	
Corpus width M1	Ardipithecus ramidus	1	1.00
	Australopithecus anamensis	1	2.00
	Australopithecus afarensis	8	7.44
	Australopithecus africanus	9	17.56
	Paranthropus boisei	16	32.97
	Paranthropus robustus	6	18.83
	Total	41	
Postcanine tooth area P3-M3	Ardipithecus ramidus	3	2.00
	Australopithecus anamensis	2	6.00
	Australopithecus afarensis	2	7.00
	Australopithecus africanus	3	8.00
	Paranthropus boisei	6	15.83
	Paranthropus robustus	3	13.00
	Total	19	
Molar tooth area M1-M3	Ardipithecus ramidus	3	2.00
	Australopithecus anamensis	2	6.00
	Australopithecus afarensis	2	7.00
	Australopithecus africanus	3	8.67
	Paranthropus boisei	7	16.14
	Paranthropus robustus	3	13.00
	Total	20	

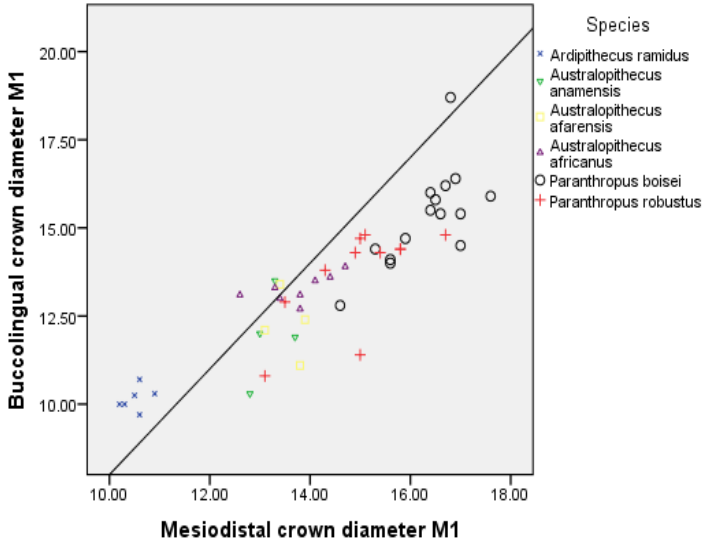

Figure 8. *Compare of MD-BL M1 on Specimens*

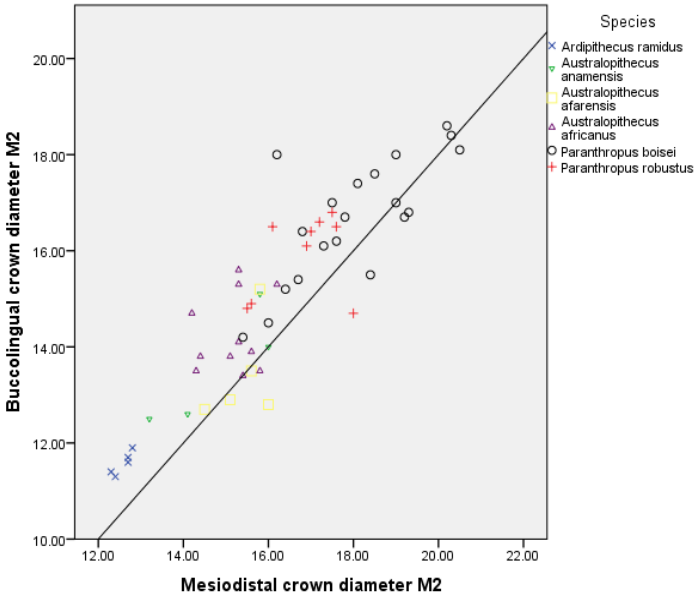

Figure 9. *Compare of MD-BL M2 on Specimens*

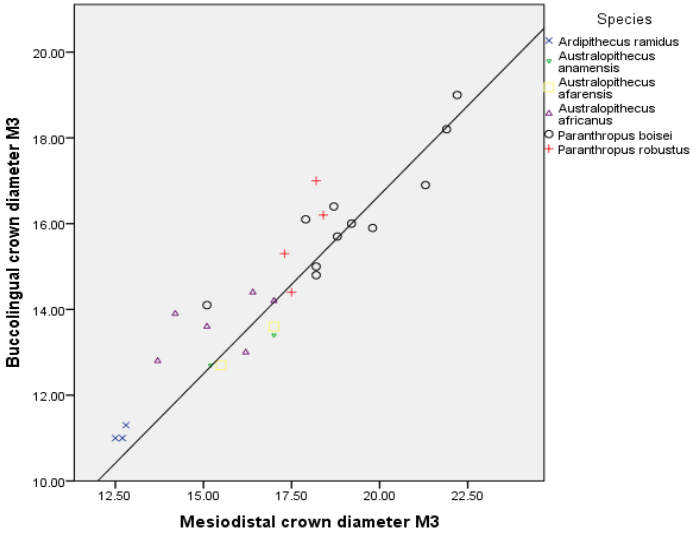

Figure 10. *Compare of MD-BL M3 on Specimens*

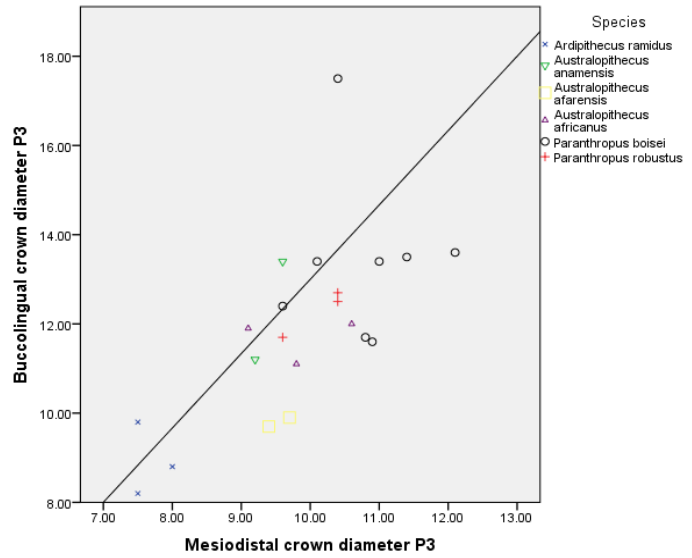

Figure 11. *Compare of MD-BL P3 on Specimens*

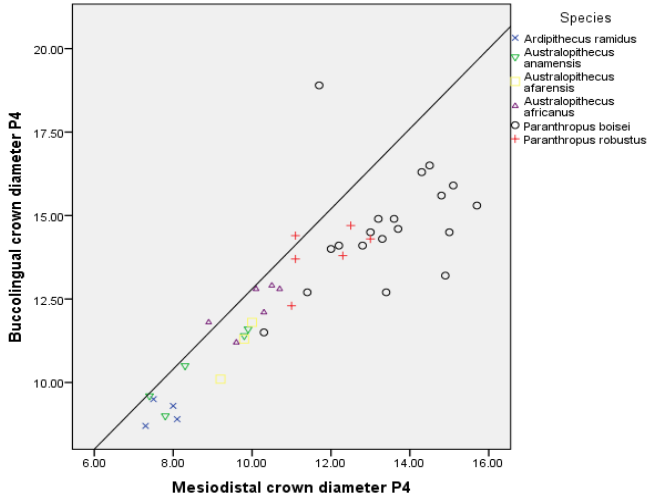

Figure 12. *Compare of MD-BL P4 on Specimens*

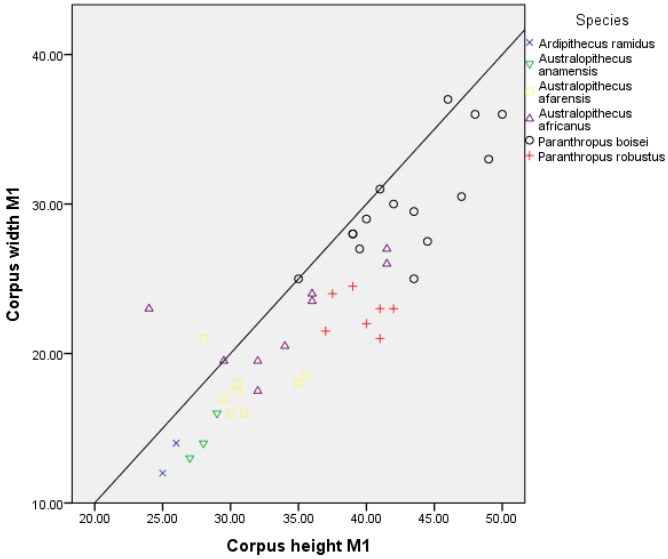

Figure 13. *Compare of Corpus Height and Width M1 on Specimens*

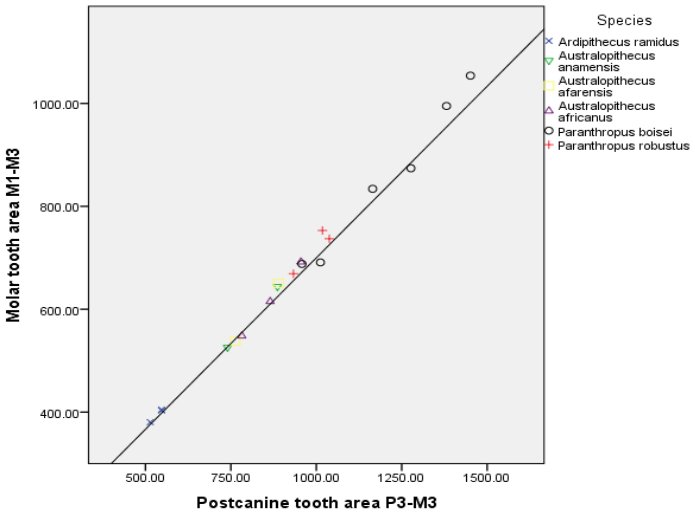

Figure 14. *Compare of Molar Tooth Area and Post-canine Tooth Area on Specimens*

As the shown in the figures above (8-14), there is a dramatic increase in the size of the tooth measurements in all specimens.

Secondly, as the Kruskal-Wallis Test is observed in terms of habitat, we can report that the rank table indicates the mean rank of the mesiodistal and buccolingual diameter (P3-M3) and corpus height and width M1 for each habitat groups *(table 3)*. In this mean rank, open woodlands, bushlands and edaphic grasslands are larger values than other habitat groups. The mean rank of all the variables (mesiodistal and buccolingual diameter (P3-M3) and corpus height and width M1) for each habitat group can be used to compare the effect of the different habitat.

Table 3. Mean Rank of Masticatory Anatomy Characters on Habitat in the Kruskal-Wallis Test

Habitat

	Habitat	N	Mean Rank
Mesiodistal crown diameter M1	Forest/closed woodlands	6	3.50
	Open woodlands	4	11.88
	Open woodlands, bushlands, edaphic grassland	55	37.75
	Total	65	
Mesiodistal crown diameter M2	Forest/closed woodlands	5	3.00
	Open woodlands	5	15.20
	Open woodlands, bushlands, edaphic grassland	49	34.27
	Total	59	
Mesiodistal crown diameter M3	Forest/closed woodlands	3	2.00
	Open woodlands	2	12.00
	Open woodlands, bushlands, edaphic grassland	32	21.03
	Total	37	
Mesiodistal crown diameter P3	Forest/closed woodlands	3	2.00
	Open woodlands	2	6.75
	Open woodlands, bushlands, edaphic grassland	19	14.76
	Total	24	
Mesiodistal crown diameter P4	Forest/closed woodlands	4	3.75
	Open woodlands	5	8.20
	Open woodlands, bushlands, edaphic grassland	38	28.21
	Total	47	
Buccolingual crown diameter M1	Forest/closed woodlands	6	3.75
	Open woodlands	4	13.25
	Open woodlands, bushlands, edaphic grassland	39	29.47
	Total	49	
Buccolingual crown diameter M2	Forest/closed woodlands	5	3.00
	Open woodlands	4	14.50
	Open woodlands, bushlands, edaphic grassland	49	33.43
	Total	58	
Buccolingual crown diameter M3	Forest/closed woodlands	3	2.00
	Open woodlands	2	8.25
	Open woodlands, bushlands, edaphic grassland	24	17.19
	Total	29	
Buccolingual crown diameter P3	Forest/closed woodlands	3	2.00
	Open woodlands	3	12.50
	Open woodlands, bushlands, edaphic grassland	20	15.38
	Total	26	
Buccolingual crown diameter P4	Forest/closed woodlands	4	3.00
	Open woodlands	6	8.50
	Open woodlands, bushlands, edaphic grassland	35	27.77
	Total	45	
Corpus height M1	Forest/closed woodlands	1	2.00
	Open woodlands	1	3.50
	Open woodlands, bushlands, edaphic grassland	38	21.43
	Total	40	
Corpus width M1	Forest/closed woodlands	1	1.00
	Open woodlands	1	2.00
	Open woodlands, bushlands, edaphic grassland	39	22.00
	Total	41	
Postcanine tooth area P3-M3	Forest/closed woodlands	3	2.00
	Open woodlands	2	6.00
	Open woodlands, bushlands, edaphic grassland	14	12.29
	Total	19	
Molar tooth area M1-M3	Forest/closed woodlands	3	2.00
	Open woodlands	2	6.00
	Open woodlands, bushlands, edaphic grassland	15	12.80
	Total	20	

Table 4. The Test Statistic Table of Masticatory Anatomy on Habitat

Test Statistics[a,b]

	Chi-Square	df	Asymp. Sig.
Mesiodistal crown diameter M1	23.094	2	.000
Mesiodistal crown diameter M2	19.107	2	.000
Mesiodistal crown diameter M3	9.385	2	.009
Mesiodistal crown diameter P3	9.953	2	.007
Mesiodistal crown diameter P4	18.956	2	.000
Buccolingual crown diameter M1	19.812	2	.000
Buccolingual crown diameter M2	18.130	2	.000
Buccolingual crown diameter M3	9.844	2	.007
Buccolingual crown diameter P3	8.060	2	.018
Buccolingual crown diameter P4	21.222	2	.000
Corpus height M1	4.868	2	.088
Corpus width M1	5.583	2	.061
Postcanine tooth are P3-M3	9.383	2	.009
Molar tooth area M1-M3	9.617	2	.008

a) Kruskal-Wallis Test

b) Grouping variable: Habitat

A Kruskal-Wallis test showed that there was a statistically significant difference in the masticatory anatomy between the different habitat groups in the *table 4*, p = between *0.000* and *0.088*, and the mean rank of habitat is shown in *table 3*. It has been seen to be highest rank of all values in open woodlands, bushlands and edaphic grasslands. In other words, each specimen groups have different type of habitat compared with

their masticatory anatomy. On the other hand, the distribution of masticatory anatomy, according to the habitat groups of specimens can be observed in the figure below:

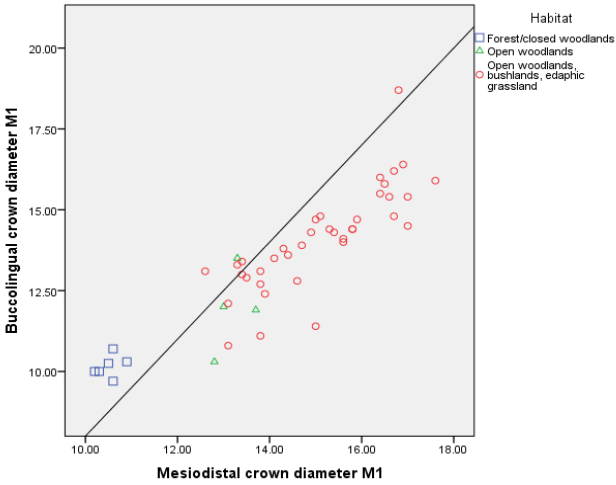

Figure 15. *Compare of MD-BL M1 on Habitat of Specimens*

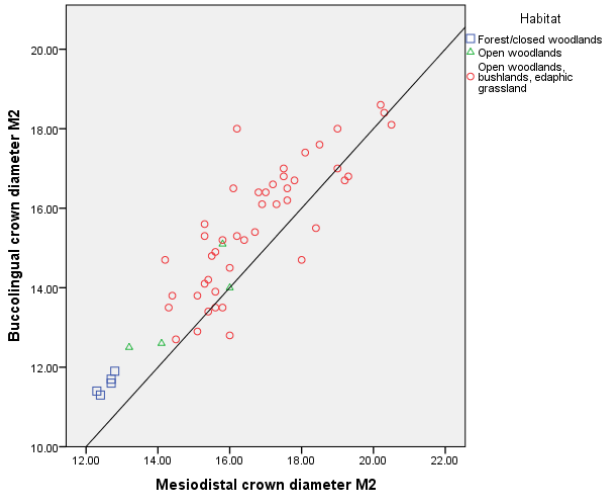

Figure 16. *Compare of MD-BL M2 on Habitat of Specimens*

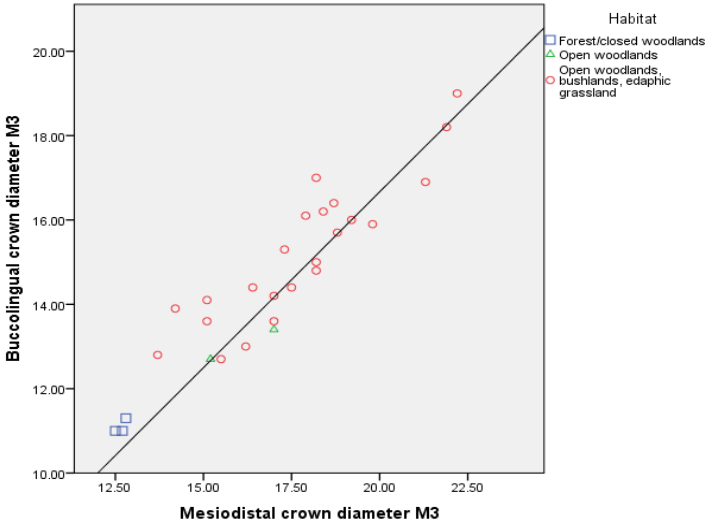

Figure 17. *Compare of MD-BL M3 on Habitat of Specimens*

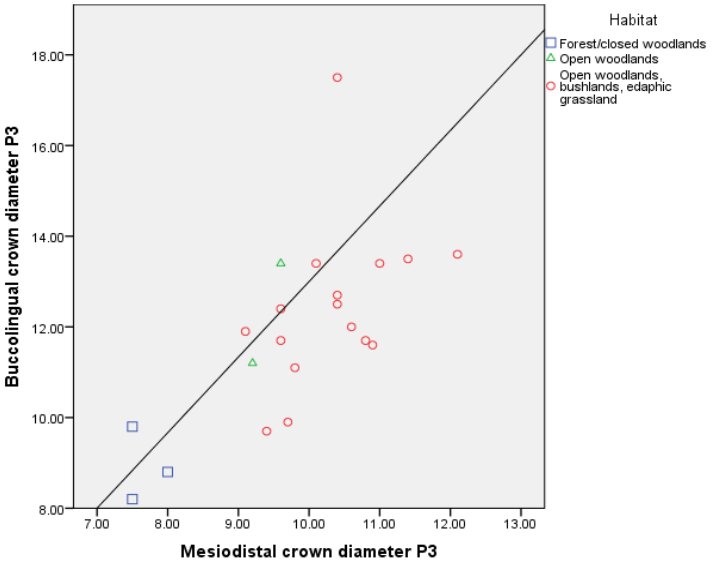

Figure 18. *Compare of MD-BL P3 on Habitat of Specimens*

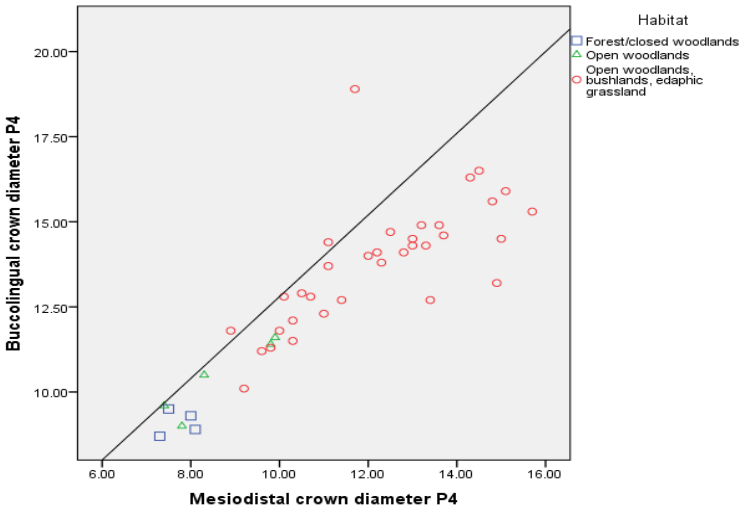

Figure 19. *Compare of MD-BL P4 on Habitat of Specimens*

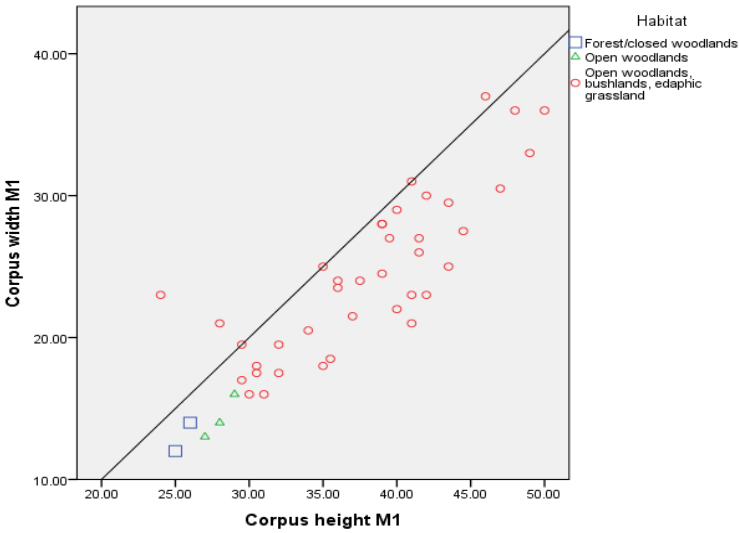

Figure 20. *Compare of Corpus Height and Width M1 on Habitat of Specimens*

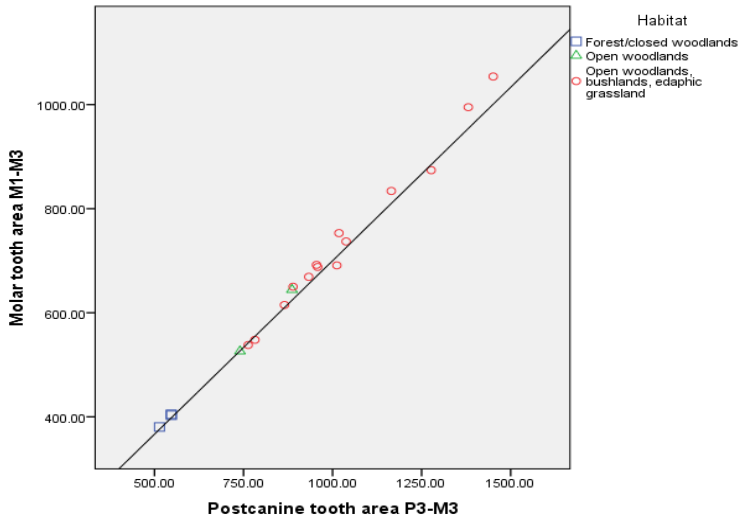

Figure 21. *Compare of Molar Tooth Area and Post-canine Tooth Area on Habitat of Specimens*

As shown in the figures above (15-21), there is a dramatic increase in the size of the tooth measurements, according to different habitat groups of specimens.

Finally, as the Kruskal-Wallis Test is observed in terms of the diet of specimens, we can report that the rank table indicates the mean rank of the mesiodistal and buccolingual diameter (P3-M3) and corpus height and width M1 for each diet groups (*table 5)*. In this mean rank, C_4 plants, hard or abrasive foods are larger in values than other diet groups. The mean rank of all variables (mesiodistal and buccolingual diameter (P3-M3) and corpus height and width M1) for each diet group can be used to compare the effect of the different diet.

Table 5. Mean Rank of Masticatory Anatomy Characters on Diet in the Kruskal-Wallis Test

Ranks

	Diet	N	Mean Rank
Mesiodistal crown diameter M1	C3 plants, soft foods and fruits	6	3.50
	C4 plants	19	17.63
	C4 plants, hard foods and corrosive	40	44.73
	Total	65	
Mesiodistal crown diameter M2	C3 plants, soft foods and fruits	5	3.00
	C4 plants	21	17.95
	C4 plants, hard foods and corrosive	33	41.76
	Total	59	
Mesiodistal crown diameter M3	C3 plants, soft foods and fruits	3	2.00
	C4 plants	10	10.15
	C4 plants, hard foods and corrosive	24	24.81
	Total	37	
Mesiodistal crown diameter P3	C3 plants, soft foods and fruits	3	2.00
	C4 plants	7	9.07
	C4 plants, hard foods and corrosive	14	16.46
	Total	24	
Mesiodistal crown diameter P4	C3 plants, soft foods and fruits	4	3.75
	C4 plants	16	12.34
	C4 plants, hard foods and corrosive	27	33.91
	Total	47	
Buccolingual crown diameter M1	C3 plants, soft foods and fruits	6	3.75
	C4 plants	17	17.97
	C4 plants, hard foods and corrosive	26	34.50
	Total	49	
Buccolingual crown diameter M2	C3 plants, soft foods and fruits	5	3.00
	C4 plants	20	17.40
	C4 plants, hard foods and corrosive	33	40.85
	Total	58	
Buccolingual crown diameter M3	C3 plants, soft foods and fruits	3	2.00
	C4 plants	10	10.95
	C4 plants, hard foods and corrosive	16	19.97
	Total	29	
Buccolingual crown diameter P3	C3 plants, soft foods and fruits	3	2.00
	C4 plants	8	12.88
	C4 plants, hard foods and corrosive	15	16.13
	Total	26	
Buccolingual crown diameter P4	C3 plants, soft foods and fruits	4	3.00
	C4 plants	15	12.93
	C4 plants, hard foods and corrosive	26	31.88
	Total	45	

Table 6. The Test Statistic Table of Masticatory Anatomy on Diet

Test Statistics[a,b]

	Chi-Square	df	Asymp. Sig.
Mesiodistal crown diameter M1	42.572	2	.000
Mesiodistal crown diameter M2	38.186	2	.000
Mesiodistal crown diameter M3	21.055	2	.000
Mesiodistal crown diameter P3	12.750	2	.002
Mesiodistal crown diameter P4	34.401	2	.000
Buccolingual crown diameter M1	28.896	2	.000
Buccolingual crown diameter M2	37.505	2	.000
Buccolingual crown diameter M3	14.719	2	.001
Buccolingual crown diameter P3	8.640	2	.013
Buccolingual crown diameter P4	30.005	2	.000

a) Kruskal-Wallis Test

b) Grouping variable: Diet

A Kruskal-Wallis test showed that there was a statistically significant difference in the masticatory anatomy between the different diet groups in the *table 6*, p = between *0.000* and *0.013*, and the mean rank of habitat is shown in *table 5*. It has been seen to be the highest rank of all values in C_4 plants, hard or abrasive foods. In other words, each specimen groups has different habitat and diet when compared with their masticatory anatomy. On the other hand, the distribution of masticatory

anatomies, according to diet groups of specimens is observed in the figure below:

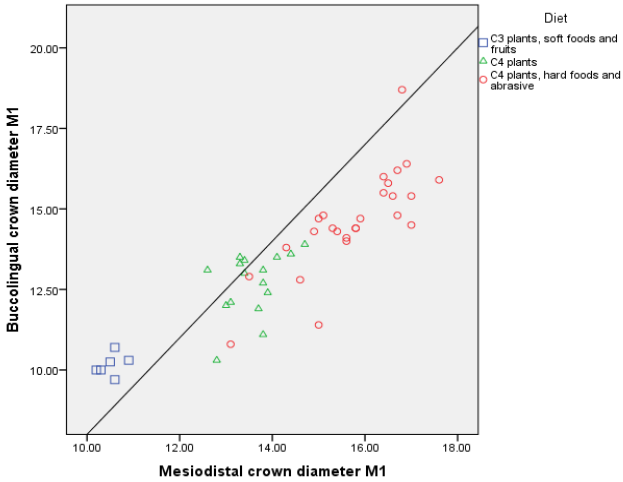

Figure 22. *Compare of MD-BL M1 on Diet of Specimens*

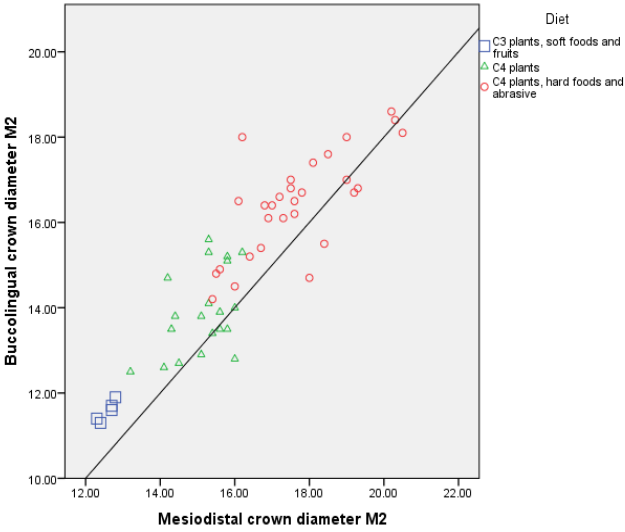

Figure 23. *Compare of MD-BL M2 on Diet of Specimens*

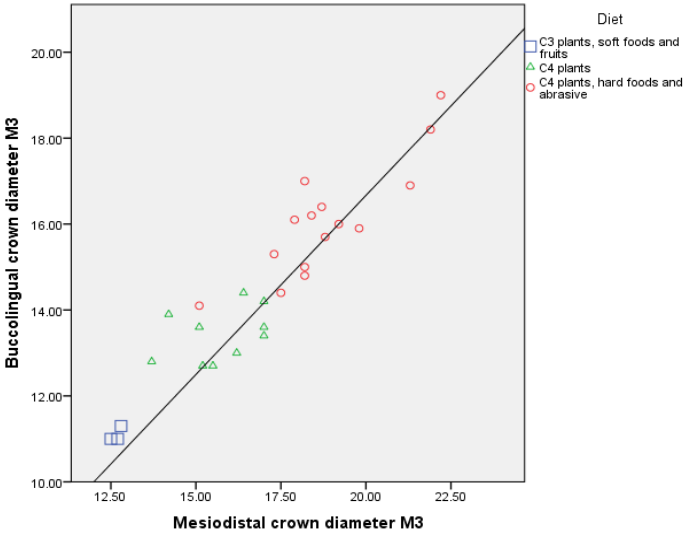

Figure 24. *Compare of MD-BL M3 on Diet of Specimens*

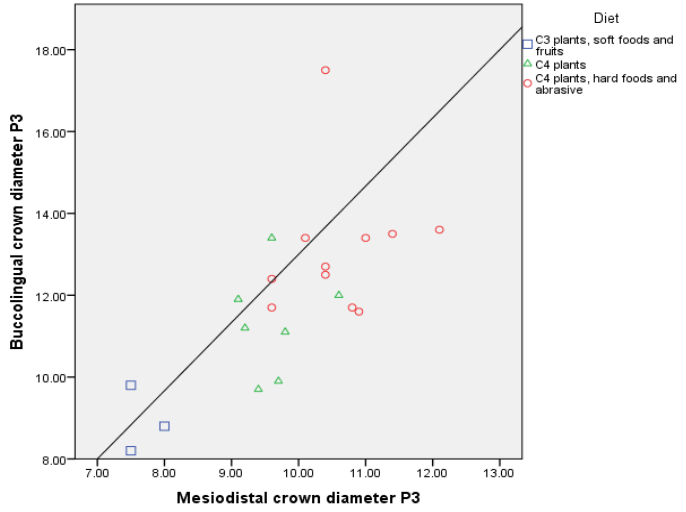

Figure 25. *Compare of MD-BL P3 on Diet of Specimens*

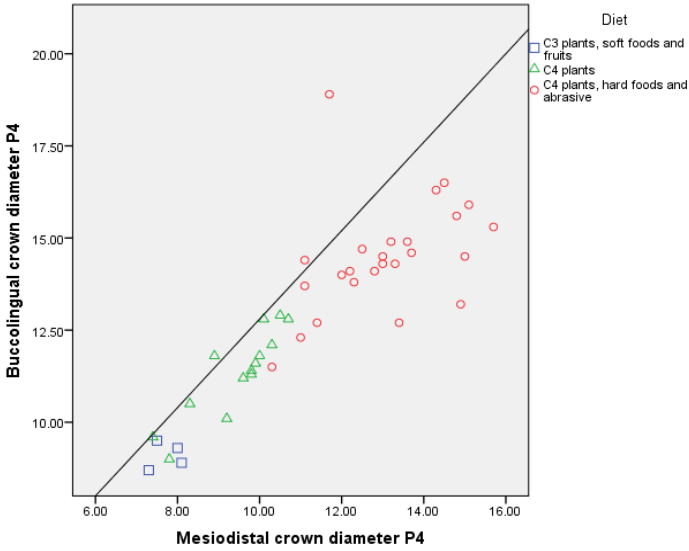

Figure 26. *Compare of MD-BL P4 on Diet of Specimens*

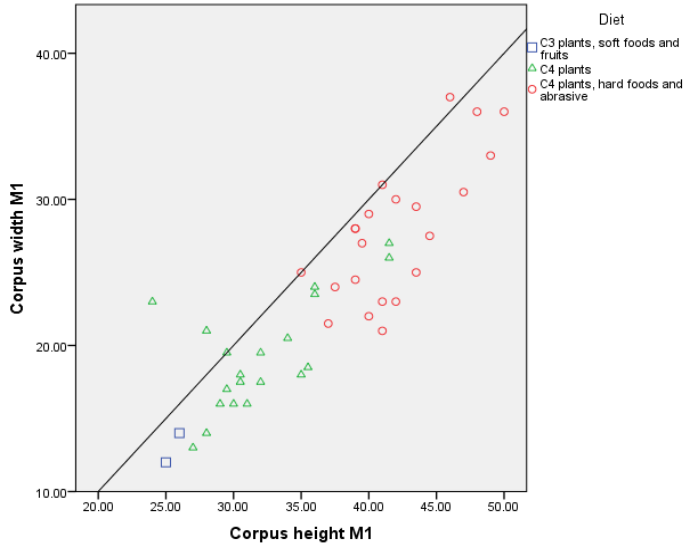

Figure 27. *Compare of Corpus Height and Width M1 on Diet of Specimens*

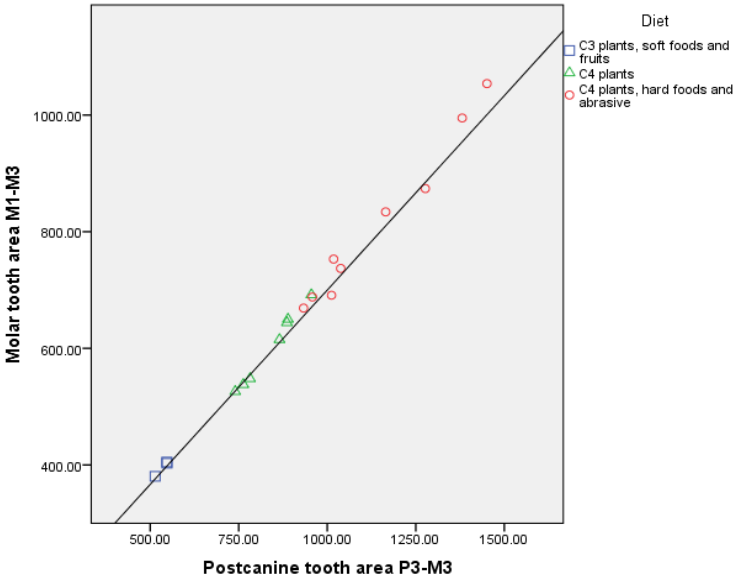

Figure 28. *Compare of Molar Tooth Area and Post-canine Tooth Area on Diet of Specimens*

It can be seen that there is a dramatic increase in the size of the tooth measurements according to different diet groups of specimens (figure 22-28).

Analysis of Variance test is performed to see whether mandibular robustucity differed based on the type of habitat levels amongst specimens, dividing specimens' habitat into three independent groups (forest/closed woodland, open woodlands and open woodlands, bushlands and edaphic grasslands). When examined the descriptive table, corpus height/width is increased from forest/closed woodlands to open woodlands, bushlands and edaphic grasslands as parallel manner (*table 7*).

Table 7. Distribution on Habitats of Mandibular Robustucity

Descriptives

		N	Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Minimum	Maximum
						Lower Bound	Upper Bound		
Corpus height M1	Forest/closed woodlands	2	25.5000	.70711	.50000	19.1469	31.8531	25.00	26.00
	Open woodlands	3	28.0000	1.00000	.57735	25.5159	30.4841	27.00	29.00
	Open woodlands, bushlands, edaphic grassland	39	37.9744	6.27647	1.00504	35.9398	40.0090	24.00	50.00
	Total	44	36.7273	6.88903	1.03856	34.6328	38.8217	24.00	50.00
Corpus width M1	Forest/closed woodlands	2	13.0000	1.41421	1.00000	.2938	25.7062	12.00	14.00
	Open woodlands	3	14.3333	1.52753	.88192	10.5388	18.1279	13.00	16.00
	Open woodlands, bushlands, edaphic grassland	40	24.4500	5.651340	.88756	22.6547	26.2453	16.00	37.00
	Total	45	23.2667	6.29177	.93792	21.3764	25.1569	12.00	37.00

Then, Anova table is performed and the table shows the output of the ANOVA analysis and whether we have a statically significant difference between our mean groups (*table 8*). We can see that the significance level of corpus height and corpus width is 0.002 and 0.001 (p= .002 and p= .001), which is below 0.05. Therefore, there is a statically significant difference in the mean of corpus height and width M1 between the different types of habitat.

Table 8. Level of Significance of Mandibular Robustucity

Anova

		Sum of Squares	df	Mean Square	F	Sig.
Corpus height M1	Between Groups	541.25	2	270.626	7.400	.002
	Within Groups	1499.47	41	36.573		
	Total	2040.72	43			
Corpus width M1	Between Groups	506.23	2	253.117	8.604	.001
	Within Groups	1235.56	42	29.418		
	Total	1741.80	44			

Table 9. Post-hoc Test between Habitat and Mandibular Robustucity

Multiple Comparisons

Tukey HSD

Dependent Variable	(I) Habitat	(J) Habitat	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
						Lower Bound	Upper Bound
Corpus height M1	Forest/closed woodlands	Open woodlands	-2.50000	5.52061	.893	-15.9242	10.9242
		Open woodlands, bushlands, edaphic grassland	-12.47436*	4.38452	.019	-23.1360	-1.8127
	Open woodlands	Forest/closed woodlands	2.50000	5.52061	.893	-10.9242	15.9242
		Open woodlands, bushlands, edaphic grassland	-9.97436*	3.62334	.023	-18.7851	-1.1637
	Open woodlands, bushlands, edaphic grassland	Forest/closed woodlands	12.47436*	4.38452	.019	1.8127	23.1360
		Open woodlands	9.97436*	3.62334	.023	1.1637	18.7851
Corpus width M1	Forest/closed woodlands	Open woodlands	-1.33333	4.95128	.961	-13.3624	10.6958
		Open woodlands, bushlands, edaphic grassland	-11.45000*	3.92996	.015	-20.9978	-1.9022
	Open woodlands	Forest/closed woodlands	1.33333	4.95128	.961	-10.6958	13.3624
		Open woodlands, bushlands, edaphic grassland	-10.11667*	3.24677	.009	-18.0047	-2.2286
	Open woodlands, bushlands, edaphic grassland	Forest/closed woodlands	11.45000*	3.92996	.015	1.9022	20.9978
		Open woodlands	10.11667*	3.24677	.009	2.2286	18.0047

*. The mean difference is significant at the 0.05 level.

This is great to know, but we do not know which of the specific groups differed. Fortunately, we can find this out in the Multiple Comparisons Table (9), which includes the results of post-hoc test. As the multiple comparisons table is examined above, it can be seen that this table shows which groups differed from each other. From the results so far, we know that there are significant differences between the groups as a whole. This table shows that there is a significant difference in the corpus height M1 between the habitat groups living in forest/closed woodlands and open woodlands, bushlands and edaphic grasslands (*p= 0.019*), as well as between the open woodlands and open woodlands, bushlands and edaphic grasslands (*p= 0.023*). However, there were no differences between the groups that are living in forest/closed woodlands and open woodlands (*p= 0.893*). In a similar way, there is a significant difference in the corpus width M1 between the habitat groups living in forest/closed woodlands and open woodlands, bushlands and edaphic grasslands (*p= 0.015*), as well as between the open woodlands and open woodlands, bushlands and edaphic grasslands (*p= 0.009*). However, there were no differences between the groups living in forest/closed woodlands and open woodlands (*p= 0.961*).

Then, Analysis of Variance test is performed again to see whether mandibular robustucity differed based on the type of diet levels amongst specimens, dividing specimens' diet into three independent groups (C_3 plants, soft foods, fruits, C_4 plants and C_4 plants, hard and abrasive foods). When examined the

descriptive table, corpus height/width is increased from C_3 plants, soft foods, fruits to C_4 plants, hard and abrasive foods as parallel manner (*table 10*).

Table 10. Distribution on Diet of Mandibular Robustucity

Descriptives

		N	Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Min.	Max.
						Lower Bound	Upper Bound		
Corpus height M1	C3 plants, soft foods and fruits	2	25.5000	.70711	.50000	19.1469	31.8531	25.00	26.00
	C4 plants	20	32.0250	4.52907	1.01273	29.9053	34.1447	24.00	41.50
	C4 plants, hard foods and abrasive	22	42.0227	4.01923	.85690	40.2407	43.8048	35.00	50.00
	Total	44	36.7273	6.88903	1.03856	34.6328	38.8217	24.00	50.00
Corpus width M1	C3 plants, soft foods and fruits	2	13.0000	1.41421	1.00000	.2938	25.7062	12.00	14.00
	C4 plants	20	19.2750	3.82676	.85569	17.4840	21.0660	13.00	27.00
	C4 plants, hard foods and abrasive	23	27.6304	4.73914	.98818	25.5811	29.6798	21.00	37.00
	Total	45	23.2667	6.29177	.93792	21.3764	25.1569	12.00	37.00

Then, Anova table is performed and the table shows the output of the ANOVA analysis and whether we have a statically significant difference between our mean groups (*table 11*). We can see that the significance level of corpus height and corpus width is 0.000 and 0.000 (p= .000 and p= .000), which is below

0.05. Therefore, there is a statically significant difference in the mean of corpus height and width M1 between the different types of diet.

Table 11. Level of Significance of Mandibular Robustucity

ANOVA

		Sum of Squares	**df**	**Mean Square**	**F**	**Sig.**
Corpus height M1	Between Groups	1311.251	2	655.626	36.849	.000
	Within Groups	729.476	41	17.792		
	Total	2040.727	43			
Corpus width M1	Between Groups	967.454	2	483.727	26.237	.000
	Within Groups	774.346	42	18.437		
	Total	1741.800	44			

Table 12. Post-hoc Test between Habitat and Mandibular Robustucity

Multiple Comparisons

Tukey HSD

Dependent Variable	(I) Diet	(J) Diet	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
						Lower Bound	Upper Bound
Corpus height M1	C3 plants, soft foods and fruits	C4 plants	-6.52500	3.12820	.105	-14.1317	1.0817
		C4 plants, hard foods and abrasive	-16.52273*	3.11525	.000	-24.0979	-8.9475
	C4 plants	C3 plants, soft foods and fruits	6.52500	3.12820	.105	-1.0817	14.1317
		C4 plants, hard foods and abrasive	-9.99773*	1.30320	.000	-13.1667	-6.8288
	C4 plants, hard foods and abrasive	C3 plants, soft foods and fruits	16.52273*	3.11525	.000	8.9475	24.0979
		C4 plants	9.99773*	1.30320	.000	6.8288	13.1667
Corpus width M1	C3 plants, soft foods and fruits	C4 plants	-6.27500	3.18438	.132	-14.0114	1.4614
		C4 plants, hard foods and abrasive	-14.63043*	3.16544	.000	-22.3209	-6.9400
	C4 plants	C3 plants, soft foods and fruits	6.27500	3.18438	.132	-1.4614	14.0114
		C4 plants, hard foods and abrasive	-8.35543*	1.31280	.000	-11.5449	-5.1660
	C4 plants, hard foods and abrasive	C3 plants, soft foods and fruits	14.63043*	3.16544	.000	6.9400	22.3209
		C4 plants	8.35543*	1.31280	.000	5.1660	11.5449

*. The mean difference is significant at the 0.05 level.

This Multiple Comparisons table (12) shows that there is a significant difference in the corpus height M1 between the diet groups feeding with C_3 plants, soft foods, fruits and C_4 plants, hard and abrasive foods (*p= 0.000*), as well as between the C_4 plants and C_4 plants, hard and abrasive foods (*p= 0.000*). However, there were no differences between the groups that are feeding with C_4 plants and C_3 plants, soft foods, fruits (*p= 0.105*). In a similar way, there is a significant difference in the corpus width M1 between the diet groups feeding with C_3 plants, soft foods, fruits and C_4 plants, hard and abrasive foods (*p= 0.000*), as well as between the C_4 plants and C_4 plants, hard and abrasive foods (*p= 0.000*). However, there were no differences between the groups feeding with C_4 plants and C_3 plants, soft foods, fruits (*p= 0.132*).

The Principal Components analysis is performed at the final stage to understand the relationship on different masticatory anatomies of specimens and discuss the differences between the variables.

According to results, as shown in the correlation matrix table (*table 13*), all variables are positively and significantly correlated with each other. The highest correlation is found between the mesiodistal crown diameter M2 and buccolingual crown diameter M3, with a correlation value of *.950*. The correlation between the mesiodistal crown diameter M3 and the mesiodistal crown diameter M2, and mesiodistal crown diameter M3 and buccolingual crown diameter M3 is following the values of *.943* and *.939*.

Table 13. Correlation Matrix of Masticatory Anatomy Characters

Correlation Matrix

		Mesiodistal crown diameter M1	Mesiodistal crown diameter M2	Mesiodistal crown diameter M3	Mesiodistal crown diameter P3	Mesiodistal crown diameter P4	Buccolingual crown diameter M1	Buccolingual crown diameter M2	Buccolingual crown diameter M3	Buccolingual crown diameter P3	Buccolingual crown diameter P4
Correlation	Mesiodistal crown diameter M1	1.000	.891	.851	.866	.898	.914	.886	.867	.803	.877
	Mesiodistal crown diameter M2	.891	1.000	.943	.882	.934	.776	.900	.950	.643	.769
	Mesiodistal crown diameter M3	.851	.943	1.000	.865	.918	.798	.890	.939	.701	.824
	Mesiodistal crown diameter P3	.866	.882	.865	1.000	.885	.750	.824	.878	.693	.778
	Mesiodistal crown diameter P4	.898	.934	.918	.885	1.000	.793	.899	.929	.704	.861
	Buccolingual crown diameter M1	.914	.776	.798	.750	.793	1.000	.917	.781	.881	.936
	Buccolingual crown diameter M2	.886	.900	.890	.824	.899	.917	1.000	.868	.813	.917
	Buccolingual crown diameter M3	.867	.950	.939	.878	.929	.781	.868	1.000	.669	.778
	Buccolingual crown diameter P3	.803	.643	.701	.693	.704	.881	.813	.669	1.000	.895
	Buccolingual crown diameter P4	.877	.769	.824	.778	.861	.936	.917	.778	.895	1.000

Table 14. KMO and Bartlett's Test

Kaiser-Meyer-Olkin Measure of Sampling Adequacy.		.827
Bartlett's Test of Sphericity	Approx. Chi-Square	293.732
	df	45
	Sig.	.000

As illustrated in above *table 14*, the overall Measure of Sampling Adequacy (MSA) for the set of variables is *.827*, which exceeds the minimum requirement of *0.50* for overall MSA. The next requirement is the probability relating to Bartlett's Test of Sphericity. It should be less than the level of significance. In this regard, as seen in the table above, the Bartlett test is found $p<0.000$, that is to say, it is significant.

Table 15. Total Variance Explained of Masticatory Anatomy of Specimens

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings			Rotation Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	8.618	86.180	86.180	8.618	86.180	86.180	5.254	52.536	52.536
2	.701	7.013	93.193	.701	7.013	93.193	4.066	40.657	93.193
3	.191	1.912	95.105						
4	.146	1.462	96.567						
5	.113	1.130	97.697						
6	.089	.893	98.590						
7	.067	.673	99.262						
8	.053	.527	99.790						
9	.014	.139	99.929						
10	.007	.071	100.000						

Extraction Method: Principal Component Analysis.

The total variance explained in the *table 15* above indicates that the first factor has the value of 86.1%, while the second factor has the value of 7.0% by chosen measurement. The components explain 93.193% of the total variance in the variables, which are included on the components, that is to say, these 2 factors and 10 different masticatory anatomies explained the relationship of each specimen. This percentage of variance explained 60% or more of the total original variance in the variables.

Table 16. Rotated Component Matrixa on Masticatory anatomy of Specimens

	Component	
	1	**2**
Mesiodistal crown diameter M2	.905	.387
Buccolingual crown diameter M3	.886	.403
Mesiodistal crown diameter M3	.849	.457
Mesiodistal crown diameter P4	.841	.483
Mesiodistal crown diameter P3	.818	.441
Mesiodistal crown diameter M1	.693	.658
Buccolingual crown diameter M2	.682	.680
Buccolingual crown diameter P3	.323	.908
Buccolingual crown diameter M1	.490	.841
Buccolingual crown diameter P4	.513	.829

Extraction Method: Principal Component Analysis.

Rotation Method: Varimax with Kaiser Normalization.

a. Rotation converged in 3 iterations.

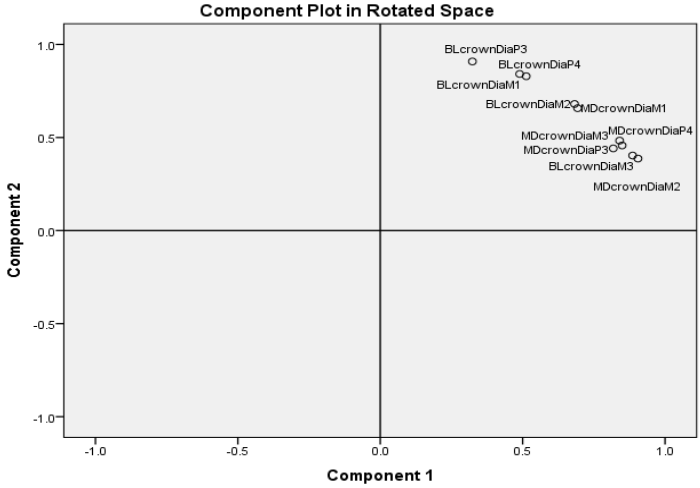

Figure 29. *Component Plot in Rotated Space on Masticatory Anatomy of Specimens*

As shown in the *table 16* above, there are nine variable loads on the first components, the mesiodistal crown diameter M1-M2-M3-P3-P4 and the buccolingual crown diameter M1-M2-M3-P4. The second component includes the following variables: the buccolingual crown diameter M1-M2-M3-P3-P4 and the mesiodistal crown diameter M1-M3-P3-P4. The MD crown diameter M1-M3-P3-P4 and the BL crown diameter M1-M2-M3-P4 are complex variables, which have a substantial loading on both the first and second component (it can be seen also in *figure 29*). The reason is that either be treated as a component of the variable that loads highest on, i.e. the first factor, or is omitted from all components. In our view, the loading of these variables on the second factor is almost as large as that on

the first factor, and the concept of the variable is closer to the construct of the second factor.

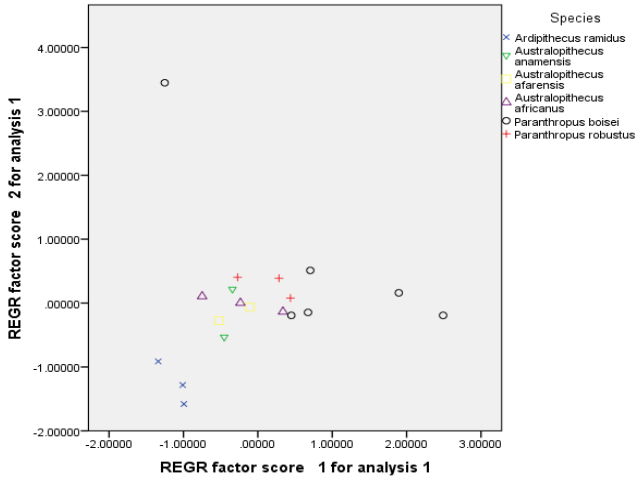

Figure 30. *Factor Score of Masticatory Anatomy of Specimens*

As a result, our data confirm the effect of different habitats and diet on different masticatory anatomies of specimens, that is to say, each different habitat and diet has different masticatory anatomy.

2.3. Discussion

The environmental/climatic changes in the Pliocene are one of the most problematic and very interesting points due to their effects on dietary (habitat) ecology and the masticatory anatomy of *Ardipithecus*, *Australopithecus* and *Paranthropus*. It can be seen that this point associates with cranial and dental morphology, dietary ecology and the environmental changes during early hominids.

As the early hominid specimens in the Plio-Pleistocene period are observed, it can be seen that there were differences between them in terms of their masticatory anatomy. It has been also seen in our analysis. This probable arises from habitat/ dietary change, that is to say, when the habitat or diet changed, specimens masticatory anatomies changed in a parallel manner. It is not yet confirmed whether the main reason is climate change. The reason of change of specimens' masticatory anatomies is that it might be arises from morphological changes in evolutionary process. Therefore, researchers evaluate all the factors simultaneously, such as combined of diet, habitat and specimens' masticatory anatomies. On the other hand, changing of environment is not such a surprising result. Role of the habitat (dietary) change in the evolutionary process is very important, since this change affected the tooth shaping directly or indirectly. Therefore, our researches like most researches in early hominin diets are based on tooth shape, tooth size, enamel thickness and the mandibular structure, as these points can provide some clues in certain cases. For example, thanks to tooth size, as through it, food size can be learned. For instance, if the specimens used to feed on small food items, they would have small incisors. However, if the specimens used to feed on larger food items, they would have large incisors. In a similar way, tooth shape can provide the food characteristics (hardness, toughness and deformability). Another point is enamel thickness, which is related to the consumption of hard, soft and corrosive food items. For instance, the enamel thickness of the earliest hominin

was thin and they had smaller molars than *Australopithecus*, and also *Paranthropus*, suggesting fleshy fruits and soft leaves diet. In other respects, the craniodental structure of *Australopithecus*, which is large, flat cheek teeth and low relief molars, thickly enameled and heavily mandibles, represents a dietary habit changes, that is to say, while it is dominated by soft forest items, like fruits, after that, it is started to dominate hard and brittle seeds or nuts together with existence of open areas in Plio-Pleistocene (increased) (Teaford and Ungar, 2000; Suwa, 2009). In addition, our analysis shows that together with the change of specimens' diet and habitat, dramatic increase in the size of the specimens' masticatory anatomy took place. This increase might be related to habitat change. Of course, it can be seen that there was a change on specimens' habitat so their masticatory anatomies are affected. Nevertheless, what was the main reason for such changes in specimens' masticatory anatomy? Diet, habitat or morphological changes in evolutionary process? It is no doubt that some climatic conditions were changed from the Miocene to the Pleistocene period. Before the changes, there were warm weather conditions and forest/closed woodland area in Africa, but, together with shift, The Ice Age started, so the region of Africa was affected by the glacial factors and covered with drier and more open environments. In the meantime, Africa was covered with C_3 plants (trees, bushes, forbs), related to forest and shrubland, but there was no evidence of the presence of C_4 plants (tropical grasses and some sedges). Then, it C_4 items were detected along with coming open habitat. Hence,

early hominid dietary habits started to change and also affected tooth morphology, indirectly. However, even though these changes have been clearly seen, its effect on the hominin tooth morphology is still discussed and researched. Nevertheless, the reconstruction of the early hominin habitat and the effect that this had on the tooth morphology has recently contributed to especially the stable isotopes analysis and the microwear studies. Some conventional opinions supported that there was a change in their diet/habitat ecology, which in turn affected their masticatory anatomy; others explained that there were no continuous trends in their habitat system, so these changes are not associated with their masticatory anatomy.

As the recent studies on early hominids dietary habits are examined, it can be seen that both the microwear studies and the stable isotopes have provided very important information about diet and paleoecology (subtle, sort-term alteration, and reflect the specific seasons and climatic conditions). Thanks to microwear studies, the surface fractal complexity will be learned (pitting) or the shift in apparent roughness with scale of investigation (scratch rate). Hard and brittle food items caused pitting (tooth wear), while tough items (leaves or meat) led to scratches (Ungar, 2010). According to this microwear result, *Ardipithecus ramidus* did use to eat hard or brittle items. Although, the craniodental features of *Au. anamensis* show feeding on hard and brittle items, the microwear analysis indicates that they did not feed on hard items, but instead on soft items. In other words, the craniodental characteristics on

early hominins may not show their dietary habits. Then, when *Au. afarensis* are observed, it can be seen that it has a complex structure, that is to say, their fine scratch is like a gorilla, whereas their pits and microflakes are like a baboon because of the variety of food sources. Next, the microwear studies of *Au. africanus* demonstrate that it has a small pit and scratch like *Au. afarensis*. Nevertheless, the pitting rate on *Au. africanus* is higher than *Au. afarensis*, due to the quality of food. Also, a specific quantity of grit in their diet was found (Grine 1981). According to this database, *Australopithecus africanus* and other early hominins fed on plants and these plants were clearly hard and gritty. Underground storage organs (both C_3 and C_4 bulbs and rhizomes) would fit this data, but specimens showing a higher degree of C_4 isotope values may have chosen underground storage organs from grasses. When *Au. africanus* is compared with *Paranthropus robustus*, *Paranthropus robustus* is larger than *Au. africanus*, in terms of microwear complexity. In addition, *Paranthropus robustus* had the maximum complexity rate and the minimum anisotropy rate (Scott, 2005) because of consuming very hard and brittle foods. Finally, *Paranthropus boisei* had elongated feeding with tough or fibrous food items, perhaps with comparatively small dietary worth instead of the consumption of hard items (Walker, 1981). However, the last microwear studies on *Paranthropus boisei* give a surprising result. It is found that it does not have large or heavy pitting rate, in contrast, fine scratches are available. This result is similar to *Au. anamensis* and *afarensis*, as well as tough items grazers. In

other words, *Paranthropus boisei* did not feed on hard items. This situation cannot be possible because they had major and powerful masticatory anatomy and mandibular robustucity, so it should be related to corrosive and hard food items. It can be seen also in our analysis. Corpus height/width is increased from C_3 plants, soft foods, fruits to C_4 plants, hard and abrasive foods as parallel manner. Therefore, it should be feed on hard items like C_4 plants. According to this result, there is a discrepancy between them. What is the reason for the difference between microwear studies and the craniodental characteristics? It is not known, but it should be examined in another important analysis in order to obtain a reliable result.

The stable isotope analysis provided relative rate of plants, using the C_3 (whole trees, shrubs, temperate environmental conditions and bush land) or C_4 (in subtropical areas and contain grass and reeds in temperate areas, and a limited number of dry or sline-adapted shrubs) food for early hominin. According to the stable isotopes analysis, the habitat of *Ardipithecus ramidus* was open savanna grassland, as well as riparian woodland and forests areas (Cerling et al., 2010). *Ardipithecus ramidus* diet is different from other early hominins, which included a significant quantity of C_4 resources. Although the habitat of *Ardipithecus ramidus* consisted of C_4 resources, it preferred C_3 plants (fruits and leaves) sources and the $\delta^{18}C$ values of *Ardipithecus ramidus* show that their habitat was a wooded and they did not consume C_4 foods. What was the reason for them to prefer the C_3 plants? It is not yet known. The habitat

of *Au. anamensis* was dry and semi-dry climatic factors. The stable isotopic analysis on soil demonstrates that their fauna (African savanna) is composed of mainly C_4 plants with trees and bush about 60-80%. The habitat of *Au. afarensis* was a complex structure. Their location consisted of closed to open forest, bush land and grassland with seasonal flows and rivers. It is predicted that their diet consisted of brittle foods and the carbon isotope analysis values are higher than *Ardipithecus ramidus*. The habitat of *Au. africanus* was a mosaic, including riparian woodland, edaphic grassland and bushland. The isotopic analysis indicates that the mosaic forest area is formed with notable land of C_4 grasses and the reconstructed *fauna* reconstructional fauna. The diet of *Australopithecus africanus* consisted of some C_4 isotopes (Sponheimer& Lee-Thorp 1999). Grass and sedges, involving their seeds, roots, and leaves, end up with C_4 isotope signs in enamel, as does feeding animals that feed on those plants. Van der Merwe et al. (2003) believe that the diet of *Australopithecus africanus* was based on grass, sedges, or meat resources, while Sponheimer and Lee-Thorp (1999) suggest that *Australopithecus africanus* fed on meat from grazing animals. Even though there were plenty of the C_4 plants in Africa 1.8 million years ago, these plants (grasslands) have been available ever since the Miocene period. Also, the carbon isotope values on the enamel thickness show that *Au. africanus'* diet was comprised of C_4 sources of around 35-40%, while the dominant component was by C_3 resources (65%), which is another surprise. Why did *Australopithecus africanus* prefer

C_4 resources, instead of C_3 items? It is not yet known, but it is probably because of the habitat change. In other words, it started with C_3 items (leaves and fruits) then inclined to C_4 resources, such as, reeds and grasses. *Paranthropus robustus'* habitat was open grassland or open savanna and their diet was complex. The carbon isotope analysis provided surprising results again about the diet of *Paranthropus*. The carbon isotope components of *Paranthropus robustus* and *Paranthropus boisei* are different from each other. Their diet was not comprised of just one type of food, including C_3 and C_4 (heavily 35-40%). It is estimated that although it fed on basically C_3 items, such as fruits and nuts, it also fed on significant quantities of $C_{4,}$ like sedges and grasses. On the other hand, the habitat of *Paranthropus boisei* was a wet habitat, with a riverine forest or woodland area related to extensive edaphic grasslands. The carbon isotopes analysis demonstrates that they clearly consumed C_3 items, as well as C_4 sources. However, $\delta^{13}C$ values show that their diet consisted of C_4 items about 77%. Together with that, it is clearly stated that *Paranthropus specimens'* habitat was comprised of C_4 items.

Researchers have tried to find a logical relationship between hominid dietary (habitat) evolution and climatic changes (Vrba 1995; Potts 1998). Many studies focused on origin of Homo, but they could not find any existing relationship with each other, until the early hominids diet had been investigated. There was slow cooling and drying climate conditions during the Miocene, so a rise in microhabitat variability might be seen. These involved river and lake margins, bush lands, woodland

and savanna. Potts (1998) stated that locomotors action was an important factor for early hominids in environmental conditions. This versatility needs to be extended to the dietary factor of early hominids, as well. In general, the craniodental features of the early hominids provide an advantage in short or long-term climatic changes on source availability.

Deciding the diet of early specimens is a paramount point for reconstructing its paleoecology, because the quantity and quality of food objects might have affected their postcranial, cranial, mandible and tooth structures, with association with their production, eating and mastication, these anatomical attributes have been intensively studied.

In this research, we tried to bring a new perspective to the reconstruction of early specimens habitat/diet, according to climatic/environmental changes and reflect their masticatory anatomies. There is no doubt that it almost impossible to reach an exact conclusion on the early specimens dietary habit and their tooth morphology, according to environmental changes. However, we found important data to assume that according to PCA and other analyses, the masticatory anatomy of *Ardipithecus ramidus*, *Australopithecus anamensis*, *afarensis* and *africanus*, *Paranthropus boisei* and *robustus* is changed according to habitat and diet groups. It is also worth mentioning as a conclusion that these tooth characteristics are related to each other. In addition, all of the factors are related with each other. Of course, morphological changes in evolutionary process were affected these factors, but habitat and diet' role is more important

than other factor. On the other hand, the main problems are still unsolved, in regard to the main reason of environmental change and if these environmental changes had affected the specimens' masticatory anatomies, directly or indirectly. These questions and much more are waiting to be answered.

2.4. Conclusions

The effects of the climatic and environmental changes during the Pliocene and whether they are associated with the diet/habitat ecology and if there is a relationship between the dietary/habitat ecology and the masticatory morphology of *Ardipithecus*, *Australopithecus* and *Paranthropus* are thoroughly discussed in this study. This project has explained the following points:

- Climatic/ environmental changes occurred from the warm Miocene through the Pleistocene period, and so habitat/diet of specimens was affected.
- Together with environmental changes, Africa was covered with open woodland and grassland (C_4 plants), while there was a forest/closed woodlands area (C_3 plants).
- The masticatory anatomy of the specimens has also shown differences from each other and it is probably arising from the habitat/dietary changes.
- There was a dramatic increase on the size of the masticatory anatomy of the specimens from forest/closed woodland to open woodland, bush land and edaphic grassland and also from C_3 items to C_4 items.

- All of the factors, such as diet, habitat, craniofacial and masticatory anatomy are related with each other.

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