Taxonomy and paleoecology of the Pleistocene Equidae from Makuyuni, Northern Tanzania

Dominik Wolf, Sherry V. Nelson, Hilde L. Schwartz, Gina M. Semprebon, Thomas M. Kaiser & Raymond L. Bernor

Abstract

The Pleistocene equid material found at Makuyuni, Tanzania, is diverse. Despite the poor preservation of the specimens, there is measurement data evidence that the site features at least two species of *Equus* and at least one species of hipparionine horse (genus *Eurygnathohippus*). Taxonomic comparisons suggest a horse fauna similar to that seen in the Daka Member of the Bouri Formation in Ethiopia. Mesowear and microwear as well as stable carbon and oxygen isotopes analyses indicate that all Makuyuni equids fed predominantly on C_4 grasses, but that browse was an important component of their diet as well; as evidenced by microwear, the diet must also have been rich in grit. *Eurygnathohippus* is marked by an overall more abrasive paleodiet than *Equus*. There is evidence that the putative larger species of *Equus* preferred a diet similar to the hipparionine horses, whereas the smaller form of *Equus* preferred shorter and possibly less coarse grasses. Serial carbon and oxygen isotope sampling reveals climate shifts. Some of the isotope data indicates that the smaller species of *Equus* might have migrated.

K e y w o r d s : Equidae, Makuyuni, taxonomy, mesowear, microwear, stable isotopes.

Zusammenfassung

Das Pleistozäne Equiden-Material von Makuyuni, Tansania, ist divers. Trotz des schlechten Erhaltungszustandes der Exemplare deuten Messdaten darauf hin, dass die Fundstelle mindestens zwei Spezies der Gattung *Equus* und eine Hipparion-Spezies (Gattung *Eurygnathohippus*) aufweist. Taxonomische Vergleichsstudien legen eine Pferde-Fauna nahe, die der Fauna der Daka-Subformation der Bouri-Formation in Äthiopien ähnelt. Mesowear- und Microwear-Analysen sowie stabile Kohlenstoff- und Sauerstoff-Isotopen-Untersuchungen zeigen, dass alle Equiden von Makuyuni sich vorwiegend von C_4 -Gräsern ernährten, aber dass Blattnahrung ebenfalls ein wichtiger Nahrungsbestandteil war. Die Untersuchung von Microwear deutet darüber hinaus darauf hin, dass die Nahrung reich an Staub war. *Eurygnathohippus* bevorzugte Nahrung, die insgesamt abrasiver als die von *Equus* war. Die größere der beiden *Equus*-Spezies nahm vermutlich Nahrung zu sich, die der der hipparionen Pferde ähnelte, während die kleinere *Equus*-Spezies kürzeres und möglicherweise weniger raues Gras bevorzugte. Serielle Kohlenstoff- und Sauerstoff-Isotopen-Beprobung zeigt saisonale Klimaveränderungen an. Ein Teil der Isotopen-Untersuchungsergebnisse lässt außerdem vermuten, dass die kleinere *Equus*-Spezies jahreszeitlich bedingt gewandert seien mag.

Contents

1.	Introduction	250
2.	Materials and methods	250
	2.1. Material	250
	2.2. Morphological description and taxonomic assessment	251
	2.3. Terminology	251
	2.4. Mesowear analysis	251
	2.5. Microwear analysis	252
	2.6. Stable isotope analysis	252
3.	Sedimentology, taphonomy, and chrono- and biostratigraphy of the Makuyuni vertebrate localities	253
4.	Makuyuni equid taxonomy	254
	4.1. <i>Equus</i> sp	255
	4.1.1. Equus sp. large species	255
	4.1.2. Equus sp. small species	257
	4.1.3. Taxonomic remarks	258
	4.2. Eurygnathohippus sp.	260
	4.2.1. Taxonomic remarks	
5.	Paleodietary and paleoecological assessment	264
	5.1. Mesowear analyses	264
	5.2. Microwear analysis	264
	5.3. Carbon and oxygen isotopes analyses	264
6.	Summary and conclusions	
7.	References	
Ap	pendix	

1. Introduction

The Plio-Pleistocene sedimentary rocks of the Lake Manyara region within the southern Gregory Rift, Northern Tanzania, have been known for their fossil vertebrate content since the early 20th century works of JÄGER (1913), RECK (1921), and RECK & KOHL-LARSON (1936). LOUIS and MARY LEAKEY subsequently discovered Pleistocene sediments at the western tributary of the Makuyuni River, which were then investigated e.g. by KENT (KENT 1941; 1942). The Makuyuni River and its tributaries, which drain part of the area east of Lake Manyara, progressively cut into Pleistocene sedimentary rocks due to recent erosion. Recent exploration of the Lake Manyara region undertaken by BROMAGE, SCHRENK, KAISER, and SEIFFERT resulted in the discovery of new fossil localities and excavation work in the area around the village of Makuyuni between 1993 and 1995 (KAISER et al. 1995; KAISER 1997, 2000; KAISER et al. 2010). The exposed sedimentary rocks have been shown to contain abundant vertebrate fossil remains at several outcrops. The equid material described herein was collected at MK4, a rich fossil locality at the southwestern limit of the village Makuyuni (Fig. 1). The locality is known for its rare skeletal and dental remains of Lower Paleolithic hom-



inids as well as their stone artifacts. The Makuyuni mammalian fauna furthermore includes the families Suidae, Hippopotamidae, Bovidae, Rhinocerotidae, Elephantidae, and Equidae (KAISER et al. 2005, 2010). The Makuyuni equid fauna interestingly comprises both late hipparions (genus *Eurygnathohippus*) and horses of the genus *Equus*, likely constituting one of the later occurrences of hipparionine horses (cf. e. g. GILBERT & BERNOR 2008). Both genera are represented by dental and postcranial material (cf. KAISER et al. 2010); however, only the dental material was available for this study.

In this paper, we report on our taxonomic assessment of the equid fauna from Makuyuni and provide morphological descriptions of representative teeth for each tooth position; the problem of potential stratigraphic mixing as well as the time interval the equid material from Makuyuni likely represents are discussed in a separate section of this study. We furthermore analyzed paleodietary preferences evident in the equid dental material by performing macroscopic facet development (mesowear) analysis (FORTELIUS & SOLOUNIAS 2000) and low magnification stereoscopic microwear analysis (SOLOUNIAS & SEMPREBON 2002). Additional paleodietary information and insight into the paleoeocolgy at Makuyuni was gained by sampling selected teeth for stable carbon and oxygen isotopes.

Abbreviation

HCRP Hominid Corridor Research Project

Acknowledgements

We are grateful to the Government of Tanzania (Department of Antiquities, Dar-es-Salaam), and the Tanzania Commission of Science and Technology (COSTECH) for granting field work permission and to the University Dar-es-Salaam (especially SUSPETER MUHONGO and KAISEM MAGORI) for their support of the fieldwork through renting measuring instruments. The initiation of fieldwork in 1995, "Pliocene Biogeography of Lake Manyara, Tanzania", was made possible due to a generous grant to Dr. TIMOTHY G. BROMAGE, New York University, from the National Geographic Society, Grant# 5454-95. We would like to thank Dr. FRIEDEMANN SCHRENK, Forschungsinstitut und Naturmuseum Senckenberg, and Dr. T.G. BROMAGE for giving us permission to study the Makuyuni equid material. BER-NOR and WOLF wish to also acknowledge the National Science Foundation, including EAR-0125009 (grant to R. L. BERNOR and M. O. WOODBURNE with stipend support to D. WOLF), BCS-0321893 (grant to F. C. HOWELL and T. D. WHITE) and the Sedimentary Geology and Paleobiology Program (GEO: EAR: SEP) for supporting their research on this project. We are finally grateful to the anonymous reviewers of this manuscript, who provided useful suggestions for the improvement of our study.

2. Materials and methods 2.1. Material

Fig. 1. Geographical overview of the southern Gregory Rift and the Lake Manyara region, northern Tanzania. The asterisk indicates the location of the MK4 locality at Makuyuni (modified after KAISER et al. 2005).

The available equid material from Makuyuni consists of 91 teeth. The teeth are part of a surface collection at MK4

except for one lower molar belonging to *Eurygnathohippus*, which was found during excavation work at the site but whose identity appears to have been lost. Since the remainder of the equid material has not been excavated in-situ, it is not entirely certain to what extent the collected specimens belong to the same stratigraphic horizon or whether mixing of several levels has occurred (KAISER et al. 2010; s. below). 49 teeth belong to the genus *Equus*, 27 are hipparion teeth, and the affiliation of 15 teeth (mostly incisors) could not be determined. We provisionally allocate 23 of the *Equus* teeth to a smaller species; the remaining 26 teeth likely represent a larger *Equus* species (Fig. 2).



Fig. 2. Relative proportion of equid dental specimens separated by genus. *Equus* ssp.: n = 49; *Eurygnathohippus* sp.: n = 27; Equidae indet.: n = 15.

2.2. Morphological description and taxonomic assessment

The dental measurements taken for this study follow BERNOR et al. (1997) and BERNOR & HARRIS (2003), the measurement scheme of which is in part modified from EISENMANN (1988). We prepared bivariate plots for selected measurements for all available tooth positions and contrasted the Makuyuni data points with data presented by GILBERT & BERNOR (2008) for a comparable fauna of similar age of *Equus* and *Eurygnathohippus* from the Daka Member of the Bouri Formation in Ethiopia. Morphological description follows the pattern established by BERNOR (e. g. BERNOR et al. 1996; GILBERT & BERNOR 2008).

2.3. Terminology

We use the terms "hipparion" and "hipparionine" to refer to tridactyl horses with isolated protocones in their maxillary premolars and molars. We recognize the following genera of hipparionine horses: *Neohipparion, Nannippus*, and *Pseudhipparion* (New World), *Cormohipparion* (New World; related Old World forms are termed "*Cormohipparion*"), *Hippotherium, Hipparion, Cremohipparion, "Sivalhippus", Eurygnathohippus* (= *Stylohipparion*), *Plesiohipparion, Proboscidipparion* (Old World). These genera are discussed in e. g. MACFADDEN (1984), BERNOR et al. (1996), BERNOR & ARMOUR-CHELU (1999a, b), BERNOR et al. (2003), BERNOR et al. (2005), GILBERT & BERNOR (2008), and BERNOR & HAILE-SELASSIE (2009).

2.4. Mesowear analysis

Mesowear analyses are preferably based on second maxillary molars, which are selected in order to facilitate comparisons with data from other studies (e.g., FORTELIUS & SOLOUNIAS 2000; SOLOUNIAS & SEMPREBON 2002). The limited nature and poor preservation of the sample of Makuyuni equids, however, required extending the method to additional tooth positions. The use of maxillary fourth premolars to third molars has been tested and is now considered valid (KAISER & SOLOUNIAS 2003). We therefore followed the protocol developed by FORTELIUS & SOLOUNIAS (2000) and extended to tooth positions P4 to M3 following KAISER & SOLOUNIAS (2003).

Mesowear describes the relatively prolonged type of dental wear that is presumed to be cumulative over an individual animal's lifetime. This type of analysis is based on tooth facet development due to the relative amounts of attritive (tooth-on-tooth) and abrasive (food-on-tooth) wear imposed on dental enamel during mastication. Mesowear is assessed by examining and categorizing the shape of the buccal apex (paracone) of the respective maxillary tooth cusps in adult individuals with normal occlusion of the M1 and the M2. The method utilizes two variables: buccal apical shape of the paracone (characterized as either sharp, rounded, or blunt) and occlusal relief or the distance between paracone and metacone cusp apices and inter-cusp valleys (characterized as either high or low). Sharp apices on cusps (and hence high relief) are found when attrition dominates over abrasion (such as when relatively soft and less abrasive food items are processed). The attritive signal is masked when abrasive food items are masticated. In this latter case, relatively rounded or even blunt cusps are observed and relief is lower. A hierarchical cluster analysis was done to show similarities between fossil equid taxa and extant ungulates of known diet.

2.5. Microwear analysis

The microwear analysis was performed following the procedure developed by SOLOUNIAS & SEMPREBON (2002), which utilizes stereomicroscopy. Since only two teeth of Eurygnathohippus and a few teeth of Equus were not abraded, results are preliminary. The second enamel band of the paracone (or metacone, if necessary) of all upper molars or the protoconid of lower molars was examined. We studied microwear features of dental enamel using a light stereomicroscope and 35× magnification following the cleansing, molding, casting, and examination regime developed by SOLOUNIAS & SEMPREBON (2002). The average number of pits (rounded features) versus average number of scratches (elongated features) per taxon were assessed within a 0.4 mm square area and results compared to a database constructed from extant ungulate taxa (SOLOUNIAS & SEMPREBON 2002) to determine the dietary categories of browser versus grazer versus mixed feeder. It was also noted whether more than four large pits were present or absent per microscope field (within the 0.4 mm square area) and whether gouges were present. Scratch textures were qualitatively scored as being either predominantly fine, predominantly coarse, or a mixture of fine and coarse types of textures per tooth surface. Because of the limited material available to us for microwear analysis, results are discussed qualitatively. There is microwear data for only one specimen allocated to the larger species of Equus we recognize; we can therefore only make observations on the microwear of Equus on a more general level, considering it one taxon.

2.6. Stable isotope analysis

We sampled tooth enamel carbonate from four Eurygnathohippus and four Equus cheek teeth, all from different individuals. Two of the Equus specimens belong to the large species discussed below, the other two to the small taxon. For the two Equus individuals allocated to the small species, we sampled the teeth serially down their length from occlusal surface to root, for a length of 57 mm in HCRP-FC638 and 50 mm in HCRP-FC783. Samples of pure enamel were removed from teeth using a Dremel high-speed rotary tool with a diamond-impregnated bit. All samples were approximately 0.5–0.7 mg, and they were washed with 3 % hydrogen peroxide for 15 minutes and rinsed, followed by 0.1M acetic acid for 15 minutes and rinsed. Samples were then placed in individual borosilicate reaction vessels and reacted at 77 °C \pm 1 °C with four drops of anhydrous phosphoric acid for a total of 17 minutes in a Finnigan MAT Kiel IV preparation device coupled directly to the inlet of a Finnigan MAT 253 triple collector isotope ratio mass spectrometer. Precision and **MANYARA BEDS**



Fig. 3. Generalized stratigraphic column of the Manyara Beds. The stratigraphic position of MK4 is indicated (modified after RING et al. 2005).

accuracy of data are monitored through daily analysis of a variety of powdered carbonate standards with at least four standards reacted and analyzed daily. Measured precision is maintained at better than 0.1 ‰ for both carbon and oxygen isotope compositions.

Isotopic ratios are presented in the per mil (‰) notation

 $\delta^{13}C$ (or ¹⁸O) = (R_{sample}/R_{PDB}-1) × 1000

where R_{sample} and R_{PDB} are the ratios ${}^{13}C/{}^{12}C$ (or ${}^{18}O/{}^{16}O$) in the sample and standard respectively, and the isotope reference standard is PDB.

3. Sedimentology, taphonomy, and chrono- and biostratigraphy of the Makuyuni vertebrate localities

The Pleistocene Manyara Beds, which are exposed in the Makuyuni area and vielded the equid material here discussed, were recently described by RING et al. (2005; cf. KAISER et al. 2010). The approximately 30 m thick succession of sediments constitutes the most fossiliferous Pleistocene deposits in the Manyara Basin and consists of two subunits, informally referred to as the "lower member" and "upper member" (RING et al. 2005). The approximately 18 m-thick "lower member" features greenish-grey, relatively fine-grained marginal lacustrine deposits which overlie volcanic agglomerate. The 12-15 m-thick "upper member" is chiefly composed of reddish-brown alluvial deposits (Fig. 3). The Manyara Beds section lies non-conformably above the deeply weathered volcanic basement, but the lower-upper "member" contact is considered conformable. During the Pleistocene high stand the eastern lake margin was more than 20 km east and 100 m higher than at present, which explains that the lower-upper "member" contact can be seen at Makuyuni Village, where it is well-exposed (Fig. 4; cf. KAISER et al. 2010). The transition from "lower member" lacustrine to "upper member" alluvial deposition in the Makuyuni Beds represents a lake margin regression that may reflect one or more processes, including a southward shift in rift faulting (RING et al. 2005), aridification or an increased rate of volcaniclastic deposition on the eastern edge of the Manyara Basin.

Tuffs and tuffaceous/pumaceous strata are common in the Manyara Beds section, but of approximately fifteen volcaniclastic samples collected in 2008 only one contains volcanic feldspar grains large enough to provide a reliable radiometric date. ³⁹Ar-⁴⁰Ar analysis of that sample is currently underway at the Berkeley Geochronology Center, and results are pending. The most likely source of volcaniclastics in the Manyara Beds is Essimingor Volcano, located approximately 18 km north of Makuvuni. It is dominantly a pyroclastic volcano, and arguably the oldest volcanic center in northern Tanzania (DAWSON 2008). However, stratigraphic and petrographic analysis shows that most tuffaceous units in the Manyara Beds are stream deposits, suggesting that Essimingor eruptions delivered little or no volcanic ash to the Makuvuni region as airfall during the Pleistocene (cf. KAISER et al. 2010. Despite the presence of multiple tuffs in the section, stratigraphic correlation across the region of exposure of the Manyara Beds is challenging, as both fluvial channels and islands of crystalline basement rock punctuated the Pleistocene lake margin and disrupted depositional environments in this area.

Evaluating the faunal assemblage of 12 fossil sites of the "lower member" of the Manyara Beds, RING et al. (2005) conclude that these deposits most likely correspond to the upper Bed II and the lower Bed III at Olduvai. RING et al. (2005) likewise suggest that the "upper member" of the Manyara Beds correlate with Olduvai Bed III based on their study of nine fossil sites. We also believe that they are correlative with the Daka deposits, Ethiopia (GILBERT & BERNOR 2008).



Fig. 4. The Manyara Beds southwest of Makuyuni Village. The dashed line traces the contact between the lower and upper "members" of the section.

The MK4 locality occurs in the upper part of the lower Manyara Beds "member", approximately four meters below the lower-upper "member" contact (Fig. 4; cf. KAISER et al. 2010). The main fossiliferous horizon is a one meterthick moderately well cemented tuffaceous sandstone with ubiquitous root mottles, burrows and carbonate nodules. It grades from coarse grained and orange-colored at its base to medium grained and greenish-grey at its top. Iron oxide staining is common throughout. A grey, concretionary fossiliferous sandstone forms the base of the excavated horizon. The sandy MK4 horizon is underlain and overlain by bioturbated mudstones (Fig. 4). This upper portion of the "lower member" represents sandy shoreline and marginal mudflat facies.

In general, the fossil and artifact assemblages in the Manyara Beds show evidence of time-averaging, particu-



Fig. 5. Photo of the lower portion of a trench (GT-9), located south of and two to three meters below the MK4 locality. The dashed line traces the irregular contact of a probable footprint horizon. Similar irregular horizons occur at several stratigraphic levels in the vicinity of MK4. Jacobs staff with ten centimeter increments for scale.



Fig. 6. A recently-formed lag assemblage of bones and artifacts in an active gully on the edge of the MK4 locality. – Coin in upper right is 3 cm in diameter.

larly in the "upper member", in which assemblages have high MNI (minimum number of individuals), low taxonomic resolution, abundant rounded/polished skeletal elements, and bones with variable degrees of surface weathering. At the MK4 stratigraphic level, low sedimentation rates are implied by the predominance of fine-grained, intensively bioturbated deposits. These strata likely represent condensed horizons on which objects collected over numbers of years. Probable vertebrate footprint horizons at several stratigraphic levels below and above MK4 (Fig. 5) suggest that trampling was a dominant surface taphonomic process on such horizons during late "lower member" time. As the MK4 locality is located on a deflationary surface circumscribed and incised by active gullies, it is clear that recent erosion has also contributed to mixing and concentration of remains at the site, potentially from the upper four meters of the "lower member" and the basal portion of the "upper member" (Fig. 6).

4. Makuyuni equid taxonomy

The distinction between the genera *Equus* and *Eury*gnathohippus, respectively, in the Makuyuni equid cheek teeth sample is largely unambiguous. Only a number of specimens, which are too fragmentary, could not be allocated to either genus. *Equus* cheek teeth differ from hipparionine specimens by having a protocone that is connected to the protoloph, whereas the protocone is isolated in hipparion specimens. Makuyuni hipparions are furthermore characterized by the presence of ectostylids in their permanent mandibular dentition, as is typical for late African hipparions (cf. e. g. BERNOR & ARMOUR-CHELU 1999a, b). The identification at genus level for the incisors was in many cases not possible. We currently recognize two species of *Equus* at Makuyuni (see the taxonomic remarks below). A complete list of the specimens reflecting our current understanding of their taxonomy and the measurements taken can be found in the Appendix.

4.1. *Equus* sp. 4.1.1. *Equus* sp. large species

P2 – There is only one obvious (and possibly a second, fragmentary) P2 in this sample that can be allocated to the large species of Equus. HCRP-FC805 (Fig. 7) is a right P2 with a mesostyle height of 44.0 mm and in a middle stage-of-wear. The morphology of P2 is as follows: the parastyle is elongate and rounded; the occlusal surface of the mesostyle is square in its outline; the protocone is rounded with a strong, broad connection to the protoloph; there is a small, circular enamel ring mesial to the prefossette; the prefossette mesial wall is very simple in its plication amplitude while the distal wall is moderately complex with very short, fine plis; the postfossette mesial wall is the most complex of all fossette borders, while the postfossette distal wall has only a single pli; the hypoglyph is very shallowly incised; there is a short, simple pli caballin.

P3 – HCRP-FC553 (Fig. 8) is the only P3 we allocate to the large species of *Equus* at Makuyuni. It is a right P3 not preserved in its full height and with a square occlusal surface. Morphological features are: a partially broken mesostyle that is labially expanded and rounded; the protocone is triangular and slightly lingually indented, the connection with the protoloph labially being moderately broad but short; the mesial and distal walls of pre- and postfossette are simple, the mesial wall of the postfossette being most complex with two short plis; the hypoglyph is shallowly incised and V-shaped.

P4 – HCRP-FC526 (Fig. 9) is a left P4 with a mesostyle height of 69.5 mm and still in an early stage-of-wear. The morphology of this unusually rectangular P4 is: the occlusal portion of the mesostyle is broken; the protocone is preserved only occlusally; it is a flattened, triangular shape in its early wear, and is not complete further down the crown's length; the protocone has a weak, labially directed connection to the protoloph; the prefossette has moderate, short and fine plications of the mesial and distal walls; the postfossette has simpler plications of both the mesial and distal walls; the hypoglyph is deeply incised; there is a moderately developed pli caballin.

There is another P4, HCRP-FC550, which is more typically square in occlusal outline than HCRP-FC526, but rather poorly preserved.

M1 – HCRP-FC810 (Fig. 10) is one of five M1s. The morphology of this left molar with emergent occlusal details and a mesostyle height of 74.3 mm is: overall, the tooth has a "blocky" square appearance and is labio-lingually deep; in occlusal outline the mesostyle has a narrow, rounded appearance; the protocone is poorly preserved but has a triangular outline and has a very narrow connection to the protoloph; the prefossette mesial border is simple with one or two poorly preserved plis while the distal border is complex with several short, thin plis; the postfossette mesial border has one large pli and a number of short plis while the distal border is simple; the hypoglyph is shallow-ly incised; there is a well-developed pli caballin.

M2 - We have identified no M2s of this taxon in our sample.

M3 – There are three maxillary third molars in the sample, HCRP-FC809 being the best preserved one (Fig. 11). It is a right specimen with a mesostyle height of 40.7 mm. Morphological characteristics are: the mesostyle is relatively broad, U-shaped, and slightly angular; the protocone is oblong and somewhat flattened and shows a wavy outline; it is connected to the protoloph via a narrow stalk; the borders of pre- and postfossette are simple except for the distal border of the prefossette, which shows a number of short plis; the hypoglyph is relatively deeply incised, U-shaped, and bent lingually.

p2 – HCRP-FC851 (Fig. 12) is a right p2 with an anterostylid height of ca. 24 mm. This specimen has the following characteristics: a pointed anterostylid; the preflexid is very small, mesiodistally short and has no plis; the postflexid is elongate with a "wavy" labial margin; the metaconid is small and rounded; the metastylid is large and oblong; the linguaflexid has a small V-shape; the ectoflexid likewise has a small V-shape.

p3 – We have identified no p3s of this taxon in our sample.

p4 – There are five p4s in the sample, the best preserved one being HCRP-FC821 (Fig. 13). This right specimen has a crown height of 62.1 mm. Further characteristics are: the preflexid is relatively long and has simple margins with a characteristic, but short mesio-labial projection; the postflexid is elongate with its mesial portion being somewhat wavy and arched lingually; metaconid and metastylid are both broken occlusally, but one can see that the former is oval while the latter is smaller and more rounded; the linguaflexid is shallow and has a broad



Figs. 7–15. Maxillary and mandibular cheek teeth allocated to the large species of Makuyuni *Equus.* – Maxillary teeth (Figs. 7–11): a = labial/buccal view; b = occlusal view. **Fig.** 7. HCRP-FC805, right P2*. **Fig.** 8. HCRP-FC553. right P3*. **Fig.** 9. HCRP-FC526, left P4. **Fig.** 10. HCRP-FC810, left M1. **Fig.** 11. HCRP-FC809, right M3*. – Mandibular teeth (Figs. 12–15): a = occlusal view; b = labial/buccal view. **Fig.** 12. HCRP-FC851, right p2*. **Fig.** 13. HCRP-FC821, right p4*. **Fig.** 14. HCRP-FC862, right m2*. **Fig.** 15. HCRP-FC819, right m3*. – Left is mesial. Right specimens are mirrored (marked * above).

V-shape; the ectoflexid is deep, labially broad, but, at its tip, narrow U-shaped; there is a small pli caballinid.

HCRP-FC551 is another p4 that, given its width, may belong to the large species of *Equus* in this sample. The tooth is unusually short, though, which results in a rather square occlusal shape. It is possible that this tooth represents a further species of *Equus* in the Makuyuni sample.

m1 – There is no m1 in this sample.

m2 - Of the three m2s in the sample, HCRP-FC862 is the best preserved (Fig. 14). The crown height of this right tooth is 66.4 mm. Morphological characteristics are: the preflexid is narrow and moderately long; it shows the characteristic mesio-labial projection which here is very narrow and pointed; the postflexid is comparatively short and parallel to the lingual tooth border; the metaconid is only moderate in size and round; the metastylid is slightly smaller and more angular; the linguaflexid is broad, moderately deep, and angular-U-shaped; the ectoflexid is deep, narrow and U-shaped and touches the linguaflexid.

m3 – All four *Equus* m3s from Makuyuni likely belong to the larger species present. HCRP-FC819 (Fig. 15) is a well-preserved right specimen with a crown height of 61.5 mm. Its morphological features are: a moderately long preflexid with a distinct, triangular mesio-labial projection; the postflexid is short; the metaconid is slightly oblong and rounded; the metastylid is smaller and triangular in shape; the linguaflexid is broad, moderately deep, and U-shaped; the ectoflexid is constantly broad and U-shaped and touches the linguaflexid.

4.1.2. Equus sp. small species

P2 – There are no P2s that unambigously belong to this taxon.

P3 – We recognize four maxillary third premolars that are intermediate in size but can most likely be allocated to the smaller species of *Equus* due to their lesser width than seen in HCRP-FC553. One of the better preserved teeth is HCRP-FC785 (Fig. 16). This left specimen has a mesostyle height of 70.6 mm and is in early wear. Its other features are: the mesostyle is moderately broad but narrowing labially and somewhat angular in occlusal view; the protocone is indented lingually and therefore slightly bean-shaped; it has a narrow, distally bent connection to the protoloph; the mesial and distal walls of the pre- and postfossettes are somewhat wavy but otherwise simple with only one clear pli each; the hypoglyph is moderately incised and has a wavy appearance; there is a well-developed pli caballin.

One tooth, HCRP-FC807 is somewhat less wide and thus flatter, and more rectangular in occlusal outline than the other specimens.

P4 – There is only one, right P4 in the sample (Fig. 17). This specimen, HCRP-FC716, is remarkably small compared to the P3s described above and has a square occlusal surface. The mesostyle height is 46.0 mm; further morphological features are: the mesostyle is labially broken but lingually broad; the protocone is moderately long and slightly concave lingually; it is connected to the protoloph by a short, moderately broad stalk; the mesial wall of the prefossette and the distal wall of the postfossette are simple, whereas the distal wall of the pre- and the mesial wall of the postfossette are wavy with ca. five short plis each; the hypoglyph is moderately incised and narrow and pointed.

M1 - Of the three M1s of this species, the right specimen HCRP-FC664 (Fig. 18) is quite square in occlusal view and has a mesostyle height of 60.0 mm. Further morphological features are: the mesostyle in occlusal view is moderately broad and rounded; the protocone is oblong and slightly bean-shaped; its connection to the protoloph is constricted; the mesial wall of the prefossette has a single pli; the distal wall of the prefossette is the most complex one with a number of moderately deep plis; the mesial wall of the postfossette shows fewer but still moderately long plis, whereas the distal wall of the postfossette is simple; the hypoglyph is narrow and pointed, bent towards lingual, and moderately deep.

M2 – There are no maxillary second molars allocated to this taxon in the sample.

M3 – There are six M3s of this species at Makuyuni, the right specimen HCRP-FC606b (Fig. 19) being the smallest one and reasonably preserved at the occlusal surface; the mesostyle height cannot be given, however. Morphological features are: a narrow and V-shaped mesostyle pointing labially; the protocone is flat, oblong, and somewhat curved; its connection to the protoloph is very narrow and extends distally towards labial; the borders of preand postfossette are simple, and only the distal border of the prefossette and the mesial wall of the postfossette exhibit a single short pli; the hypoglyph is broad, angular, and moderately deep and bends far lingually.

p2; p3 – We recognize no p2s or p3s of this taxon in the sample.

p4 – Only one of the teeth, HCRP-FC789 (Fig. 20), might belong to the smaller species of *Equus* in the Makuyuni sample. This right specimen is poorly preserved, however, so that the allocation remains questionable. Full crown height cannot be given. Morphological features are: the preflexid is fragmentary mesially but appears to be moderately large, its mesio-labial projection being narrow and distinct; the postflexid is moderately elongate and slightly bent lingually; metaconid and metastylid are broken but appear well rounded; the linguaflexid is moderately large and v-shaped; the ectoflexid does not separate preand postflexid and is narrow U-shaped at its tip; there is a simple pli caballinid.

m1 – There are four m1s that we allocate to this species; the best preserved specimen being the right tooth, HCRP-FC561 (Fig. 21), which has a crown height of 59.5 mm. Its morphological features are: the preflexid is moderately long with a short but broad, labially extending projection; the postflexid is only slightly longer and extends parallel to the lingual border of the occlusal surface; the metaconid is rounded but somewhat oblong; the metastylid is smaller and more angular; the linguaflexid is broad and shallow V-shaped; the ectoflexid is deep, separating metastylid and metaconid by touching the linguaflexid; there is a small pli caballinid.

m2 - HCRP-FC578 (Fig. 22) is one of three mandibular second molars. Its crown height measures 39.0 mm. Morphological characteristics of this left m2 are: a relatively small preflexid with a weak mesio-labial projection;



Figs. 16–22. Maxillary and mandibular cheek teeth allocated to the small species of Makuyuni *Equus*. – Maxillary teeth (Figs. 16–19): a = labial/buccal view; b = occlusal view. **Fig. 16**. HCRP-FC785, left P3. **Fig. 17**. HCRP-FC716, right P4*. **Fig. 18**. HCRP-FC664, right M1*. **Fig. 19**. HCRP-FC606b, right M3*. – Mandibular teeth (Figs. 20–22): a = occlusal view; b = labial/buccal view. **Fig. 20**. HCRP-FC789, right p4*. **Fig. 21**. HCRP-FC561, right m1*. **Fig. 22**. HCRP-FC578, left m2. – Left is mesial. Right specimens are mirrored (marked * above).

an even shorter postflexid; the metaconid is relatively large, rounded, but slightly triangular in shape; the metastylid is small and rectangular; the linguaflexid is shallow and V-shaped; the ectoflexid is deep and narrow Ushaped, slightly pointing mesiolingually towards lingual and contacting the linguaflexid; there is a wavy outline indicating a pli caballinid.

m3 – There are no mandibular third molars in the sample.

4.1.3. Taxonomic remarks

The size dimensions of the teeth allocated to *Equus* exceed for many of the available tooth positions the range that is to be expected for a single species, given that intraspecific size variation for cheek teeth in equids is known to be negligible (BERNOR et al. 1997). This is particularly evident in the *Equus* M3s (Fig. 23c), for which differences in



Fig. 23. Selected bivariate plots of width/length measurements of maxillary and mandibular cheek teeth of Makuyuni *Equus.* – **a**. Maxillary P4s. **b**. Maxillary M1s. **c**. Maxillary M3s. **d**. Mandibular m2s. – Black triangles = Makuyuni; black triangles with asterisk = approximate measurement; grey squares = Daka Member of the Bouri Formation; m1 = length at occlusal level; m3 = width at occlusal level, taken across mesostyle-protocone; m8 = width of tooth across plane of metaconid and enamel band labial to protoconid. Measurements in mm.

length of more than 9 mm were observed (between HCRP-FC811 and HCRP-FC606b), the P4s (Fig. 23a), and the m2s (Fig. 23d), as can be seen in bivariate plots for width/length measurements. It is therefore highly likely that, judged by size differences alone, a minimum of two species of Equus are represented in the material from Makuyuni. The definition of the individual taxa based on the limited dental material available alone is challenging and has to be seen as preliminary at this point, as is the assumption that all taxa occurred sympatrically at the same stratigraphic level. The sample size for each available tooth position is statistically insufficient to circumscribe and validate individual taxa using standard statistical analyses/tests; however, our bivariate width/length plots yielded two distinct clusters for the maxillary cheek teeth, especially for M1 (Fig. 23b) and M3 (Fig. 23c). We used this information to help us to distinguish between provisional species where possible. Consistent morphological differences suitable to aid in this process were usually not observed. However, it appears that maxillary P3s show a more rectangular morphology in the smaller taxon, and a more square one in the large species. It was also observed that pli caballins are less well developed in maxillary cheek teeth of the smaller taxon. Our description of representative cheek teeth for each species was undertaken using well preserved specimens close to the extremes in size, i. e. the smallest specimens for the smaller species and vice versa.

There are also a number of rare teeth showing a morphology dissimilar to the rest of the sample; we have preliminarily allocated these teeth to one of the two species of *Equus* present at Makuyuni, but recognize the possibility that these specimens represent uncommon additional taxa. The respective specimens (HCRP-FC807, a P3 here allocated to the smaller species, and HCRP-FC551, a p4 preliminarily allocated to the larger species) are described in our section on the morphology of Makuyuni *Equus* cheek teeth above.

We compared the occlusal length/width measurements of Makuyuni equids with those reported for horse teeth from geographically and stratigraphically comparable Pleistocene localities in the Daka Member of the Bouri Formation in Ethiopia. Like Makuyuni, the Daka Member features both *Equus* and late hipparionine horses in its fossil record (GILBERT & BERNOR 2008), but in contrast to Makuyuni, the Daka Member specimens are better preserved and also include postcranial skeletal material.

The distribution of plotted points for occlusal width/ length measurements of *Equus* (collectively described as *Equus* sp.) from the Daka Member is similar to that of the *Equus* material from Makuyuni (Fig. 7 a–d). The Daka data points usually occur within the whole range known from Makuyuni, but most often cluster with the larger Makuyuni *Equus* teeth and frequently reach even higher size dimensions than known from the largest Makuyuni teeth; it is possible that the Daka Member features more than one species of *Equus* as well. Judged by dental material alone, the *Equus* faunas of both sites may be closely related given their overall similarity in size and comparable stratigraphic age and geographical closeness, but if so, the larger species seen at Makuyuni might have been more abundant in the Daka Member of the Bouri Formation than the smaller one.

The Makuyuni Equus material is representative of an important but insufficiently understood phase of African Equus evolution and distribution. Like the material from the Daka Member of the Bouri Formation, the Makuyuni sample is close in age to the first appearances of asses (Olduvai Bed II; CHURCHER 1982) and zebras (0.7 Ma; EISENMANN & BAYLAC 2000). We believe that the larger Makuyuni specimens might be referable to Equus oldowayensis, while the smaller ones may represent an early representative of a modern African Equus lineage; it has to be considered, however, that these species might not have occurred sympatrically. GILBERT & BERNOR (2008) argue that the Daka Member Equus (believed to be a single species) constitutes a horse at the base of the African zebra radiation and might be more closely related to Equus grevvi and E. burchelli than to E. zebra or E. quagga mainly based on observations on astragalus and metacarpal III dimensions. In consideration of our observations at Makuyuni, this might only apply to the smaller dental specimens from the Daka Member.

4.2. Eurygnathohippus sp.

P2 – The only hipparion maxillary second premolar, HCRP-FC554 (Fig. 24) is a worn right specimen with a mesostyle height of 20.2 mm. The tooth is poorly preserved; morphological features are: the parastyle is broken; the mesostyle is broad and angular labially; the isolated protocone is oblong and slightly bean-shaped; the mesial wall of the prefossette is moderately complex; the distal wall of the pre- and the mesial wall of the postfossette are similarly complex with a number of short plis; the distal wall of the postfossette is simple with apparently only a single pli; the hypoglyph is poorly preserved; there is a single, moderately long pli caballin.

P3 – There is no P3 in the sample.

P4 – HCRP-FC559 (Fig. 25) is the best preserved one of three maxillary fourth premolars. The right specimen is rather worn and has a mesostyle height of 33.4 mm. Morphological features are: the mesostyle is narrow, projects

far labially, and is angular U-shaped; the protocone is isolated, relatively flat, and oblong; the walls of pre- and postfossette are complex in their plication pattern, which is most evident at the distal wall of the prefossette with its numerous rather long plis; the hypoglyph is moderately deep incised and straight V-shaped; there are three welldeveloped pli caballins.

M1 – There are two M1s; HCRP-FC528 (Fig. 26), a left specimen, is described here. The tooth has a mesostyle height of 46.4 mm. Further characteristics are: the mesostyle is narrow with a slightly angular U-shaped labial aspect; the isolated protocone is short and flattened to indented lingually; the mesial wall of the prefossette is moderately complex; the distal wall of the pre- and the mesial wall of the postfossette are more complex, both having a number of plis which are much longer and better developed at the mesial wall of the postfossette is rather simple with only a single, long obvious pli; the hypoglyph is very shallowly incised; there is a single long pli caballin.

M2 – There are no hipparion M2s in the sample.

M3 – There are six maxillary third molars of *Eury*gnathohippus. HCRP-FC812 (Fig. 27) is a left specimen with a mesostyle height of 32.5 mm. Its characteristics are: the mesostyle is rather narrow, rounded and curves towards mesial labially; the isolated protocone is oblong and somewhat triangular; the borders of pre- and postfossettes are simple with only one or two plis except for the distal border of the prefossette which is more complex; the hypoglyph is moderately deeply incised, narrow distally, but widened mesially, and it almost encircles the hypocone; there is a long pli caballin.

p2; p3 - These positions are not represented in the sample.

p4 – Of the four mandibular fourth premolars the left specimen, HCRP-FC858 (Fig. 28) is relatively well preserved. Its crown height is 56.1 mm. Morphological features are: the preflexid is moderately long with a slightly wavy mesial aspect and a weakly developed mesio-labial projection; the postflexid is oblong and narrow and extends parallel to the lingual border of the occlusal surface; metaconid and metastylid are narrow towards the isthmus, have angular outlines, and bend sharply lingually; the linguaflexid is moderately deep, quite broad, and U-shaped; the ectoflexid is shallow and V-shaped; there is a weakly developed pli caballinid; the ectostylid is diamond-shaped in occlusal outline and located far labially on the crown.

m1 – The three unambiguous hipparion m1s display the greatest variability in size apparent in the sample from Makuyuni and might, despite broad morphological similarities, represent two different species of *Eurygnathohippus*. HCRP-FC619 (Fig. 29) is a large, right specimen in good preservation with a crown height of 53.6 mm. Morphological features are: the preflexid is quite long and concave la-



Figs. 24–31. Maxillary and mandibular cheek teeth allocated to Makuyuni *Eurygnathohippus*. – Maxillary teeth (Figs. 23–26): a = labial/buccal view; b = occlusal view. **Fig. 24**. HCRP-FC554, right P2*. **Fig. 25**. HCRP-FC559, right P4*. **Fig. 26**. HCRP-FC528, left M1. **Fig. 27**. HCRP-FC812, left M3. – Mandibular teeth (Figs. 27–30): a = occlusal view; b = labial/buccal view. **Fig. 28**. HCRP-FC858, left p4. **Fig. 29**. HCRP-FC619, right m1*. **Fig. 30**. HCRP-FC814, right m2*. **Fig. 31**. HCRP-FC620, left m3. – Left is mesial. Right specimens are mirrored (marked * above).

bially, its mesio-labial projection not being well developed; the postflexid is somewhat wavy and moderately long and extends parallel to the lingual border; metaconid and metastylid are irregular and angular in outline, the metaconid being slightly larger than the metastylid; their broader terminal portions turn markedly lingually; the linguaflexid is broad and U-shaped and rather deep; the ectoflexid is too shallow to separate pre- and postflexid, narrow to moderately broad, and U-shaped; there is one moderately developed pli caballinid; the ectostylid is large and ovate shaped.

m2 – Of the two *Eurygnathohippus* m2s, HCRP-FC814 (Fig. 30), although being damaged, exhibits the occlusal characteristics best. It is a right specimen for which

the crown height cannot be given. Its preflexid and postflexid are moderately long; the mesio-labial projection on the preflexid is inconspicuous; the postflexid is parallel to the lingual border; metaconid and metastylid are about the same size and triangular in shape, the metastylid being somewhat more oblong and pointed lingually; the linguaflexid is very broad and U-shaped; the ectoflexid is rounded but rather V-shaped and deep but does not entirely reach the linguaflexid; the specimen shows a moderately developed pli caballinid; the ectostylid is moderately large and diamond-shaped.

m3 – There are four mandibular third molars. HCRP-FC620 (Fig. 31) is a moderately well preserved left speci-

Tab. 1. Paleodietary variables for Makuyuni equid teeth. Abbreviations: N = number of specimens; Sharp = % of specimens per taxon with sharp cusp apices; Round = % of specimens per taxon with round cusp apices; Blunt = % of specimens per taxon with blunt cusp apices; High Relief = % of specimens per taxon with high relief; P = average number of pits per taxon; S = average number of scratches per taxon; LP = percentage of specimens with large pits per taxon; %F = percentage of specimens per taxon with fine scratches; %C = percentage of specimens per taxon with coarse scratches; %M = percentage of specimens per taxon with mixed scratches (fine and coarse); %G = percentage of individuals per taxon with gouges present.

			Mesowe	ar	Microwear								
Taxon	N	Sharp	Round	Blunt	High Relief	Ν	Р	S	%LP	%F	%C	%M	%G
Eurygnathohippus sp.	8	0	37.5	62.5	12.5	2	44.25	17.25	50	0	100	0	0
Equus – large species	7	14.29	42.86	42.86	0	1	54	13.5	100	0	100	0	0
Equus – small species	9	0	77.78	22.22	11.11	4	52.25	15.25	75	0	100	0	0

men with a crown height of 30.8 mm. Its features are: the preflexid is short; the postflexid is long and narrow; metaconid and metastylid are moderately large, the metaconid is triangular in shape and the metastylid is squarer; the linguaflexid is deep, broad, and angular U-shaped; the ectoflexid is very deep and has a broad contact with the linguaflexid; the ectostylid is oblong and extends distally towards labial.

4.2.1. Taxonomic remarks

The *Eurygnathohippus* material is more homogeneous in size and morphology than observed for the specimens of *Equus*. Even though there is a conspicuous variation in size for some of the tooth positions (particularly the m1s; Fig. 32a), we consider this observed variability to still be within the possible range of intraspecific variation. Since no obvious statistical clustering is evident in any of the bivariate length/width plots we prepared (e. g. for M3s; Fig. 32b), we therefore refrain from recognizing more than one species of *Eurygnathohippus*.

The Daka Member sample of *Eurygnathohippus* cf. *cornelianus* (GILBERT & BERNOR 2008) has width/length measurements similar to those observed for the Makuyuni sample (Fig. 32a, b). In consideration of the close chronological correlation and geographic proximity of the Ethiopian site and the comparable morphology and measurements, we believe that the Makuyuni hipparionine material is best referable to *Eu*. cf. *cornelianus*.

The assumption of sympatrical cooccurrence of *Equus* and *Eurygnathohippus* must remain preliminary for the reasons stated above. The in-situ discovery of a single tooth of *Eurygnathohippus* in the Manyara Beds sediments at MK4 as reported by KAISER et al. (2010), however, shows the presence of the hipparionine horses in upper "lower member" time.



Fig. 32. Selected bivariate plots of width/length measurements of maxillary and mandibular cheek teeth of Makuyuni *Eurygnathohippus.* – **a**. Mandibular m1s. **b**. Maxillary M3s. – Black triangles = Makuyuni; grey squares = Daka Member of the Bouri Formation; m1 = length at occlusal level; m3 = width at occlusal level, taken across mesostyle-protocone; m8 = width of tooth across plane of metaconid and enamel band labial to protoconid; black triangle with asterisk = approximate measurement; black triangle with cross = tooth position not certain. Measurement in mm.



Fig. 33. Cluster analysis comparing mesowear scores for the Makuyuni equids with data of extant ungulates with known diet. – **a**. Makuyuni *Equus* treated as a single taxon. **b**. Makuyuni *Equus* grouped into a large species (sp. 1) and a small species (sp. 2).

5. Paleodietary and paleoecological assessment 5.1. Mesowear analyses

Results of the mesowear analysis show that both of the Makuyuni fossil equid taxa apparently had a relatively high abrasion diet as evidenced by the high percentages of rounded and blunt cusp tips as well as low occlusal relief (Tab. 1). Eurygnathohippus generally displays coarser mesowear (blunter cusps) than the Equus species. When fossil taxa are included in a cluster analysis using extant ungulates of known diets (i.e., "typical" recent species from Fortelius & Solounias 2000), both Makuyuni equid genera cluster with extant grazers (Fig. 33a). Viewed conservatively as only one taxon, Equus on the whole clusters with extant grazers feeding on short grasses, Ceratotherium simum and Damaliscus lunatus. When the data for Equus is split into two groups (a large and a small species, Fig. 33b), the larger species clusters close to Eurygnathohippus within a group of extant grazers that are specialized for feeding on coarse grass (Bison bison as well as Equus grevyi and E. burchelli, the latter feeding on rough higher grasses). The small Equus species clusters with grazers adapted to feeding on short coarse grasses (Ceratotherium simum, which uses its flat wide mouth and prehensile lips to crop shorter coarse grasses; Damaliscus lunatus, which feeds on less coarse lower grasses). This suggests that the putative larger species of Equus preferred a dietary niche similar to the hipparions at Makuyuni.

5.2. Microwear analysis

Microwear features (e. g., pits and scratches) observed on the occlusal surfaces of enamel are the result of single occlusal events, and thus reflect diets over a much short-



Fig. 34. Scratch/pit microwear plots of Makuyuni equids in comparison to grazing and browsing morphospaces of extant ungulates with known diets. *Equus* is given as one taxon in consideration of the low number of available samples.

er duration than revealed by mesowear analysis, perhaps days or even hours before the death of the animal.

The available specimens are variable in their microwear, but mostly plot in between the extant grazing and browsing scratch/pit morphospaces or in the marginal area of the browsing morphospace. On average, the data points fall into a zone generally occupied by modern mixed feeding taxa that both browse and graze either seasonally or regionally; this pattern is similar for both equid genera at Makuyuni (Fig. 34, cf. Tab. 1). However, high numbers of pits are seen in both *Equus* and *Eurygnathohippus* relative to extant mixed feeders as well as grazers and most extant browsers with the exception of those consuming "dirty" browse (i. e., camels). This pattern is most likely indicative of grit encroachment on enamel surfaces.

5.3. Carbon and oxygen isotopes analyses

Carbon and oxygen isotopes are informative for reconstructing paleodiets and paleohabitats. Carbon isotopes distinguish between diets of graze (C₄ grasses and sedges) and browse (C₃ plants such as trees and shrubs) due to differences in photosynthetic pathways between C₄ and C₂ plants (e. g. BENDER 1971; VOGEL 1980). Additionally, plants yield a wide range of carbon and oxygen isotopic values in response to differences in light and water stress and can therefore be useful in distinguishing forest canopies, forest floors, woodlands, and open habitats (cf. NELSON 2007, and references therein). Oxygen isotopes are also useful for reconstructing paleoclimates, for water sources respond to seasonal fluctuations in precipitation and temperature (e.g. LONGINELLI 1984; QUADE et al. 1995). Isotopic analyses of fossil tooth enamel reflect an animal's diet as well as where it fed. Additionally, serial sampling of hypsodont teeth that take a year to grow can provide evidence for the annual seasonal regime an animal experienced.

C a r b o n : Carbon isotopic values in four check teeth of *Equus* and four teeth of *Eurygnathohippus* range from -2.9 to 1.8 %. This range suggests a diet dominated by C₄ grasses, with the highest values suggesting a diet of almost exclusive C₄ grasses. Mann-Whitney statistical analyses indicate no differences between *Eurygnathohippus* and *Equus* in carbon values, suggesting similar diets (Fig. 35).

Serial sampling was performed on two teeth allocated to the smaller species of *Equus* (HCRP-FC638 and HCRP-FC783). Because hypsodont equid teeth can take a year or more to develop, serial sampling can detect seasonal shifts in the animal's diet. Neither of the *Equus* teeth we sampled demonstrates seasonal shifts in diet. For each tooth, carbon values shift by no more than 0.5 ‰ throughout the length of the tooth, indicating that C_4 graze was a major



Fig. 35. Results of carbon/oxygen isotope analysis of Makuyuni equid enamel carbonate.

component of their diet throughout much or all of the year (Fig. 36).

O x y g e n : Oxygen values of tooth enamel reflect not only habitat differences but climatic shifts as well, both seasonal and over geologic time. The δ^{18} O value for regional precipitation is controlled by a number of geographic factors, such as proximity to oceans and mountains, and altitude, as well as climatic factors such as ambient temperature and amount rainfall. In tropical regions such as Tanzania, where rainfall varies but temperature remains relatively constant, oxygen monthly values reflect changes in the amount of rainfall. ¹⁸O (as part of the H₂O molecule) precipitates more readily than ¹⁶O; therefore, the more it rains, the less ¹⁸O is present in atmospheric water, and the more depleted the precipitation becomes



Fig. 36. Results of serial sampling for carbon isotopes showing intra-tooth δ^{13} C variability for two *Equus* specimens.



Fig. 37. Results of serial sampling for oxygen isotopes showing intra-tooth δ^{18} O variability for two *Equus* specimens.

(DANSGAARD 1964). Of the two Equus teeth we sampled serially (both of them allocated to the smaller species), one (HCRP-FC638) demonstrates a shift in oxygen isotopes of 2.4% throughout the length of the tooth (Fig. 37). The oxygen values at the occlusal surface are high and reflect the dry season. Oxygen values then decrease toward the root and reflect the onset of a wet season. However, another Equus tooth we sampled (HCRP-FC783) shows only a 0.5 ‰ shift throughout the length of the tooth, indicative of little to no change across the seasons. This individual may have drunk from a buffered water source such as a lake, or it may have migrated and thus dampened any seasonal shifts. Interestingly, the tooth with the least variation in oxygen (HCRP-FC783) has higher carbon values than the tooth with a seasonal oxygen shift (HCRP-FC638), averaging 1.8 ‰ vs. 0.5 ‰, suggesting that it relied more on C_{A} grasses (Fig. 36). Perhaps this individual migrated to maintain a diet of exclusive or almost exclusive C₄ grass. Future sampling of more individuals from more equid species should allow us to expand our paleoclimatic and migratory interpretations, and might shed additional light on the origins of migration in eastern Africa.

6. Summary and conclusions

The hominid locality of Makuyuni, Tanzania, features dental material of both late hipparionine horses of the genus *Eurygnathohippus* and the modern horse genus, *Equus*. Size differences in check teeth suggest that at least two species of *Equus* occur at this site. Rare premolars showing unusual morphological characteristics indicate the possible presence of further, uncommon taxa of *Equus*. The tooth sample of *Eurygnathohippus* is less variable in size and qualitative morphological features and may belong to a single species. It has to be considered, however, that condensation and stratigraphic mixing is possible at Makuyuni to some extent, so that the represented species might not have occurred sympatrically. Future stratigraphic and chronologic work should provide insight into the amount of time potentially involved in the fossil assemblage at Makuyuni.

Comparisons of the Makuyuni and the Daka Member equid assemblages suggest great similarity in their taxonomic content and age. In view of the taxon identification proposed for the Daka Member hipparion by GILBERT & BERNOR (2008), the hipparionine material at Makuyuni is best referable to *Eurygnathohippus* cf. *cornelianus*. The type specimen of *Eu. cornelianus* is from Cornelia-Uitzoek, South Africa, recently dated by magnetostratigraphy to 0.99 Ma (JAMES BRINK, personal communication to R. L. BERNOR). The larger Makuyuni *Equus* specimens may belong to *E. oldowayensis*. The smaller ones might represent an early member of a modern African *Equus* lineage. More complete material is needed to make more secure designations.

A variety of paleodietary and ecological analyses have been applied to the Makuyuni equid sample. Mesowear suggests a generally abrasive diet for both modern and hipparionine horses: Makuyuni Eurygnathohippus mesowear suggests a more abrasive diet than seen in the Equus sample. The larger Equus species and Eu. cf. cornelianus apparently grazed on relatively higher and rougher consistency grasses than the smaller species of *Equus*. The microwear signal for both Equus and Eurygnathohippus shows that browsing occurred at least occasionally and would suggest a mixed-feeding behavior with grit encroachment on food materials. When both mesowear and microwear are considered, results indicate that both Makuyuni equids apparently exploited a predominately abrasive grass-dominated diet with occasional browse supplementing grazing with considerable grit encountered in their dietary regime.

The analysis of stable carbon isotopes in enamel carbonates showed that both *Equus* and *Eurygnathohippus* largely fed on C_4 grasses, the two taxa not showing a statistically significant difference in dietary preference. Serial sampling for carbon isotopes of two *Equus* check teeth did not reveal seasonal shifts in diet. Analysis of serial oxygen samples, however, indicated seasonal shifts in one specimen. The specimen showing less seasonality was interestingly characterized by carbon isotope values suggesting a higher reliance on C_4 grasses. The animal might therefore have migrated in order to obtain its preferred diet and thus avoided the effects of seasonality.

7. References

- BENDER, M. M. (1971): Variations in the 13C/12C ratios of plants in relation to the pathway of photosynthetic carbon dioxide fixation. – Phytochemistry, 10: 1239–1245.
- BERNOR, R. L. & ARMOUR-CHELU, M. J. (1999a): Toward an evolutionary history of African hipparionine horses. – In: BROMMAGE, T. & SCHRENK, F. (eds.): African Biogeography and Human Evolution: 189–215; Oxford (Oxford University Press).
- BERNOR, R. L. & ARMOUR-CHELU, M. J. (1999b): Family Equidae. – In: RÖSSNER, G. E. & HEISSIG, K. (eds.): The Miocene Land Mammals of Europe: 193–202; Munich (Pfeil).
- BERNOR, R. L. & HARRIS, J. M. (2003): Systematics and evolutionary biology of the late Miocene and early Pliocene hipparionine horses from Lothagam, Kenya. – In: HARRIS, J. M. & LEAKEY, M. (eds.): Lothagam: The Dawn of Humanity in Eastern Africa: 387–438; New York (Columbia University Press).
- BERNOR, R. L. & HAILE SELASSIE, Y. (2009): 13. Equidae In: HAILE-SELASSIE, Y. & WOLDEGABRIEL, G. (eds.): Ardipithecus kadabba: Late Miocene Evidence from the Middle Awash, Ethiopia: 397–428; Berkeley (University of California Press).
- BERNOR, R. L., KOUFOS, G. D., WOODBURNE, M. O. & FORTELIUS, M. (1996): The evolutionary history and biochronology of European and Southwest Asian Late Miocene and Pliocene hipparionine horses. – In: BERNOR, R. L., FAHLBUSCH, V. & MITTMANN, H.-W. (eds.): The evolution of Western Eurasian Neogene mammal faunas: 307–338; New York (Columbia University Press).
- BERNOR, R. L., TOBIEN, H., HAYEK, L. A. & MITTMANN, H.-W. (1997): *Hippotherium primigenium* (Equidae, Mammalia) from the late Miocene of Höwenegg (Hegau, Germany). – Andrias, **10**: 1–230.
- BERNOR, R. L., SCOTT, R. S., FORTELIUS, M., KAPPELMAN, J. & SEN, S. (2003): Systematics and Evolution of the Late Miocene Hipparions from Sinap, Turkey. – In: FORTELIUS, M., KAP-PELMAN, J., SEN, S. & BERNOR, R. L. (eds.): The Geology and Paleontology of the Miocene Sinap Formation, Turkey: 220– 281; New York (Columbia University Press).
- BERNOR, R. L., SCOTT, R. S. & HAILE-SELASSIE, Y. (2005): A Contribution to the Evolutionary History of Ethiopian Hipparionine Horses: Morphometric Evidence from the Postcranial Skeleton. – Geodiversitas, 27: 133–158.
- CHURCHER, C. (1982): Oldest ass recovered from Olduvai Gorge, Tanzania, and the origin of asses. – Journal of Paleontology, 56: 1124–1132.
- DANSGAARD, W. (1964): Stable isotopes in precipitation. Tellus, 16: 436–468.
- DAWSON, J. B. (2008): The Gregory Rift Valley and Neogene– Recent volcanoes of northern Tanzania. – Geological Society Memoir, 33: 102 pp.
- EISENMANN, V. & BAYLAC, M. (2000): Extant and fossil *Equus* (Mammalia, Perissodactyla) skulls: A morphometric definition of the subgenus *Equus*. – Zoologica Scripta, **29**: 89–100.
- EISENMANN, V., ALBERDI, M. T., DE GIULI, C. & STAESCHE, U. (1988): Studying fossil horses, Volume 1: Methodology. – In: WOODBURNE, M. O. & SONDAAR, P. Y. (eds.): Collected papers after the "New York International Hipparion Conference, 1981": 1–71; Leiden (Brill).
- FORTELIUS, M. & SOLOUNIAS, N. (2000): Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. – American Museum Novitates, 3301: 1–36.

- GILBERT, W. H. & BERNOR, R. L. (2008): Equidae. In: GILBERT, W. H. & ASFAW, B. (eds.): *Homo erectus*: Pleistocene Evidence from the Middle Awash, Ethiopia: 133–166; Berkeley (University of California Press).
- JÄGER, F. (1913): Das Hochland der Riesenkrater und die umliegenden Hochländer Deutsch-Ostafrikas. Ergebnisse einer amtlichen Forschungsreise ins abflußlose Gebiet des nördlichen Deutsch-Ostafrika 1906/07. – Mitteilungen aus den Deutschen Schutzgebieten, Ergänzungsheft, 8: 254 pp.
- KAISER, T. M. (1997): Die Taphonomie plio-pleistozäner Hominidenfundstellen Ostafrikas mit besonderer Berücksichtigung der Säugetierfaunen des Laetoli- und Lake Manyara-Gebietes in Nordtansania. – Dissertation. Technische Hochschule Darmstadt. 284 pp.
- KAISER, T. M. (2000): Die Taphonomie plio-pleistozäner Hominidenfundstellen Ostafrikas mit besonderer Berücksichtigung der Säugetierfaunen des Laetoli- und Lake Manyara-Gebietes in Nordtansania. – Archäologische Informationen, 23: 139–142.
- KAISER, T. M. & SOLOUNIAS, N. (2003): Extending the tooth mesowear method to extinct and extant equids. – Geodiversitas, 25: 321–345.
- KAISER, T. M., BROMAGE, T. G. & SCHRENK, F. (1995): Hominid Corridor Research Project update: New Pliocene fossil localities at Lake Manyara and putative oldest Early Stone Age occurrences at Laetoli (Upper Ndolanya Beds), northern Tanzania. – Journal of Human Evolution, 28: 117–120.
- KAISER, T. M., FIEDLER, L., SCHRENK, F., SCHWARTZ, H., BROMAGE,
 T., SEIFFERT, C., SAANANE, C., KALETSCH, B., ARNHOLD, S.,
 BUSCH, S., HÜSER, A., JUNGER, B., STEINMAETZ, S., STÖTZEL, K.
 & TSCHIRSCHNITZ, C. (2005): Makuyuni, eine neue altpaläolithische Hominidenfundstelle in Tansania. – Jahrbuch des Römisch-Germanischen Zentralmuseums Mainz, 52: 1–41.
- KAISER, T. M., SEIFFERT C., HERTLER, C., FIEDLER, L., SCHWARTZ, H. L., FROST, S. R., GIEMSCH, L., BERNOR, R. L., WOLF, D., SEMPREBON, G. M., NELSON, S. V., SCHRENK, F., HARVATI, K., BROMAGE, T. G. & SANAANE, C. (2010): Makuyuni, a new Lower Palaeolithic Hominid Site in Tanzania. – Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut, **106**: 69–110.

- KENT, P. E. (1941): The recent history and Pleistocene deposits of the plateau North of Lake Eyasi, Tanganyika. – Geological Magazine, 78: 173–184.
- KENT, P. E. (1942): A note on Pleistocene deposits near Lake Manyara, Tanganyika. – Geological Magazine, 79: 72–77.
- LONGINELLI, A. (1984): Oxygen isotopes in mammal bone phosphate: a new tool for paleohydrological and paleoclimatological research? – Geochimica et Cosmochimica Acta, 48: 385–390.
- MACFADDEN, B. J. (1984): Systematics and phylogeny of *Hipparion*, *Neohipparion*, *Nannippus*, and *Cormohipparion* (Mammalia, Equidae) from the Miocene and Pliocene of the New World. Bulletin of the American Museum of Natural History, **179**: 1–196.
- NELSON, S. V. (2007): Isotopic reconstructions of habitat change surrounding the extinction of *Sivapithecus*, a Miocene hominoid, in the Siwalik Group of Pakistan. – Palaeogeography, Palaeoclimatology, Palaeoecology, 243: 204–222.
- QUADE, J., CATER, J., OJHA, T., ADAM, J. & HARRISON, T. (1995): Late Miocene environmental change in Nepal and the northern Indian subcontinent: stable isotopic evidence from paleosols. – The Geological Society of America Bulletin, 107: 1381–1397.
- RECK, H. (1921): Eine neue diluviale Säugetierfundstelle am Minjonjo in Deutsch-Ostafrika. – Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, 1–3: 25–26.
- RECK, H. & KOHL-LARSEN, L. (1936): Erster Überblick über die jung-diluvialen Tier- und Menschenfunde Dr. Kohl-Larsens im nordöstlichen Teil des Njarasa-Grabens (Ostafrika) und die geologischen Verhältnisse des Fundgebietes. – Geologische Rundschau, 27 (5): 400–441.
- RING, U., SCHWARTZ, H. L., BROMAGE, T. G. & SANAANE, C. (2005): Kinematic and sedimentological evolution of the Manyara Rift in northern Tanzania, East Africa. – Geological Magazine, 42: 355–368.
- SOLOUNIAS, N. & SEMPREBON. G. (2002): Advances in the reconstruction of ungulate ecomorphology with application to early fossil equids. – American Museum Novitates, 3366: 1–49.
- VOGEL, J. C. (1980): Fractionation of the Carbon Isotopes during Photosynthesis. 29 pp.; Berlin (Springer).

Addresses of the authors:

DOMINIK WOLF, Howard University, College of Medicine, Laboratory of Evolutionary Biology, 520 W St NW, Washington, DC 20059, USA E-Mail: dwolf@bison.howard.edu

SHERRY V. NELSON, Department of Anthropology, MSC01-1040, 1 University of New Mexico, Albuquerque, NM 87131-0001, USA HILDE L. SCHWARTZ, Earth and Planetary Sciences, UC Santa Cruz, 1156 High ST, CA 95064, USA

GINA M. SEMPREBON, Department of Biology, Bay Path College, 588 Longmeadow ST, Longmeadow, MA 01106, USA

THOMAS M. KAISER, Zoological Museum University Hamburg, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany

RAYMOND L. BERNOR, Howard University, College of Medicine, Laboratory of Evolutionary Biology, 520 W ST NW, Washington, DC 20059, USA

Manuscript received: 3 February 2010, accepted: 23 August 2010.

Appendix. List of specimens available for this study and measurements taken according to the measurement scheme modified after EISENMANN et al. (1988). Measurement numbers (m1, m2, m3, etc.) correspond to those given in BERNOR et al. (1997) and BERNOR & HARRIS (2003). Abbreviations: P = upper premolar; M = upper molar; I = upper incisor; p = lower premolar; m = lower molar; rt = right; It = left.

Specimen No.	Taxon		Element	m1	m2	m3	m4	m5	m6	m7	m8	m9	m10	m11
without no.	Equidae indet.	rt	p3 or p4			16.6	9.9	14.1		15.2			45.1	
without no.	Equidae indet.		incisor 2 (+3)	17.9	15.2	13.4		36.7						
without no.	Equidae indet.		incisor 3?	19.6?	19.2	12.0								
HCRP-FC614	Equidae indet.		incisor	17.5	15.2	13.5	14.3	28.7						
HCRP-FC534	Equidae indet.		incisor											
HCRP-FC586	Equidae indet.		incisor	14.1	11.4	13.2	12.4	27.3						
HCRP-FC584	Equidae indet.		incisor	15.1	10.3?	13.0	12.6	33.5						
HCRP-FC646	Equidae indet.		incisor	13.5	9.5	10.5	14.5	42.4						
HCRP-FC824	Equidae indet.		incisor	12.2	9.1	6.5	7.3	24.2						
HCRP-FC818	Equidae indet.		incisor	21.2?	16.8	12.5	13.1							
HCRP-FC570?	Equidae indet.		incisor											
HCRP-FC597	Equidae indet.		canine											
HCRP-FC532	Equidae indet.	lt	P or M					75.4				1		
HCRP-FC563	Equidae indet.	rt	P4?											
HCRP-FC529	Equidae indet.		M1?					68.0						
HCRP-FC851	Equus sp. large	rt	p2	33.5	31.3	15.9	7.9	16.0	18.3		12.5	16.1	24.0?	
HCRP-FC820	Equus sp. large	rt	p4	34.7		15.9			16.1					
HCRP-FC821	Equus sp. large	rt	p4	32.1	32.0	21.3	11.0	16.6	19.1	16.3	17.0	15.5	62.1	
HCRP-FC860	Equus sp. large	rt	p4	31.9	29.8	17.9	11.3	16.4	18.3	17.3	16.4	15.6	39.5?	
HCRP-FC551	Equus sp. large	lt	p4	26.0?	24.1	14.7	7.5?		19.9	17.1	19.9		33.3	
HCRP-FC576	Equus sp. large	rt	p4			17.4			15.5		13.8	13.0		
HCRP-FC852	Equus sp. large	lt	m2	29.7	27.2	16.1	8.4	10.8	17.8		14.0	13.8		
HCRP-FC806	Equus sp. large	rt	m2	30.8		16.7	9.3	10.8	15.0		14.2	12.8		
HCRP-FC862	Equus sp. large	rt	m2	28.3	27.4	15.0	8.3	9.2	18.0	16.3	15.2	12.7	66.4	
HCRP-FC531	Equus sp. large	rt	m3	32.0		14.0	9.0	8.9	13.8	12.9	12.5	9.6	50.4?	
HCRP-FC819	Equus sp. large	rt	m3	32.6	33.9	14.5	8.2	7.7	12.2	13.2	13.6	12.5	61.5	
HCRP-FC859	Equus sp. large	rt	m3	32.5		15.0	9.4	10.2	12.1	13.9	10.9	8.3		
HCRP-FC570	Equus sp. large	lt	m3			14.2								
HCRP-FC805	Equus sp. large	rt	P2	38.4	36.5	25.7	22.9	44.0	1	3	3	1	7.6	6.5
HCRP-FC546	Equus sp. large	lt	P2					29.8		0	0	0		
HCRP-FC553	Equus sp. large	rt	P3	26.9		26.8			1	0	2	0	11.2	5.1
HCRP-FC526	Equus sp. large	lt	P4	30.5		21.9		69.5	1	7	3	1	11.8	4.8
HCRP-FC550	Equus sp. large	lt	P4	29.6		26.2		45.2					13.8	
HCRP-FC557	Equus sp. large	rt	M1											
HCRP-FC810	Equus sp. large	lt	M1	28.0	25.7	28.3	31.9	74.3	1	3	1	0	11.5	5.6
HCRP-FC850	Equus sp. large	lt	M1	27.0	24.8	27.1	28.1	32.7	0	1	1	0	11.5	5.0
HCRP-FC641	Equus sp. large	rt	M1			28.2	26.8	73.6		6	1	1		6.2
HCRP-FC808	Equus sp. large	lt	M1	27.3	25.5	25.1	25.7	76.1	1	4?	3	0	11.2	4.4
HCRP-FC809	Equus sp. large	rt	M3	29.5	29.6	23.9	22.6	40.7	0	2	0	0	13.4	4.1
HCRP-FC811	Equus sp. large	lt	M3	30.7	28.4	24.8	25.1	20.2	0	4	0	0	12.7	5.4
HCRP-FC547	Equus sp. large	rt	M3	28.4	25.8	25.1		22.5?	0	0	0	0	11.4	4.8
HCRP-FC789	Equus sp. small	rt	p4			16.5		13.9	14.2	15.8		13.4		
HCRP-FC561	Equus sp. small	rt	m1	27.4	25.0	14.3	8.5	9.1	16.4	14.7	13.3	11.7	59.5	
HCRP-FC613D	Equus sp. small	rt	m1	26.6	25.1	14.3	8.2	7.7	14.3	15.2	13.9	12.3	39.4?	
HCRP-FC548	Equus sp. small	lt	ml	30.7		12.9			10.0			İ		

Appendix (continued).

Specimen No.	Taxon		Element	m1	m2	m3	m4	m5	m6	m7	m8	m9	m10	m11
HCRP-FC710	Equus sp. small	rt	m1 or m2	27.0		14.7	7.9	9.2	15.9		13.9	12.7		
HCRP-FC671	Equus sp. small	rt	m2	27.1		14.8	7.6	8.2	12.9	14.1	14.9			
HCRP-FC578	Equus sp. small	lt	m2	25.2	23.8	14.2	6.3	7.4	14.5	14.2	14.5	11.4	39.0	
HCRP-FC613B	Equus sp. small	rt	m2	27.9	26.3	15.1	7.5	11.1	15.6		14.5		55.3?	
HCRP-FC770	Equus sp. small?	rt	P2					50.5	1	7?	4	1		
HCRP-FC807	Equus sp. small	lt	P3	28.9		23.7?			1	3	5	1	8.9	
HCRP-FC785	Equus sp. small	lt	P3	27.3	23.6	25.0		70.6	1	2	1	1	9.2	5.1
HCRP-FC604	Equus sp. small	lt	P3	25.7	24.0			29.0	0	2	1	0		
HCRP-FC783	Equus sp. small	rt	P3	29.0?	26.2	25.9	25.6	66.2	1?	5?			12.4	5.2
HCRP-FC716	Equus sp. small	rt	P4	23.2	20.6	19.6?		46.0	1	5	2	1	10.5	4.9
HCRP-FC701	Equus sp. small	rt	M1	25.0		24.1		69.3	2	3	2	1	11.1	4.4
HCRP-FC664	Equus sp. small	rt	M1	24.1	21.5	24.2	24.1	60.0	1	6	3	0	10.9	4.6
HCRP-FC638	Equus sp. small	lt	M1	24.5	22.8	25.4	23.9	71.8	1	5	2	1	11.5	5.7
HCRP-FC792	Equus sp. small	rt	M3	24.2	25.0	20.0	22.3	40.3		2	1	0	13.1	3.8
HCRP-FC861	Equus sp. small	rt	M3	25.4	31.0	21.8	23.4	51.4	1	5	3	0	11.5	4.5?
HCRP-FC669	Equus sp. small	rt	M3	24.6	22.2	20.2	20.9	50.5					12.2	4.8
HCRP-FC667	Equus sp. small	rt	M3	23.1	25.9	21.2	21.8	49.1		4	2	1	11.9	4.3
HCRP-FC691	Equus sp. small	rt	M3	23.3		18.7			1	3	1			4.6
HCRP-FC606b	Equus sp. small	rt	M3	21.4		17.3			1	1	1	1	10.8	3.5
HCRP-FC533	Eurygnathohippus sp.	rt	I2	21.3	17.5	11.7	12.0	44.9						
HCRP-FC858	Eurygnathohippus sp.	lt	p4	25.3	22.9?	13.4	9.1	13.0	13.7	14.7	12.9	10.5	56.1	
HCRP-FC552	Eurygnathohippus sp.	lt	p4	25.8	22.9	13.6	8.4	12.9	12.5	14.1	12.5	10.8	46.1	
HCRP-FC816	Eurygnathohippus sp.	lt	p4	24.9		13.2	8.7	12.9	16.9	16.5?	13.3			
HCRP-FC613C	Eurygnathohippus sp.	rt	p4	22.6	22.4	13.2	8.2	11.5	13.7?	11.9	10.1			
HCRP-FC856	Eurygnathohippus sp.	rt	ml	20.8		13.4	7.2	9.8	10.9?		11.5	10.0		
HCRP-FC619	Eurygnathohippus sp.	rt	m1	26.5	24.4	15.1	10.1	13.7	15.4	14.8	12.8	12.2	53.6	
HCRP-FC857	Eurygnathohippus sp.	rt	ml	22.7	21.5	14.6	7.5	10.2	11.0	11.4	10.5	8.9	45.6?	
HCRP-FC555	Eurygnathohippus sp.	lt	m1?	25.2	23.4	14.9	8.2	11.8	12.1	13.5	11.7	10.5	42.4?	
HCRP-FC813	Eurygnathohippus sp.	rt	m2	24.6		13.7		12.7	12.4	12.9	11.5	9.9	57.9	
HCRP-FC814	Eurygnathohippus sp.	rt	m2	22.8		14.3	7.3	11.3		13.2	12.1	11.0		
HCRP-FC620	Eurygnathohippus sp.	lt	m3	27.4		14.5	6.0	11.7	12.0	11.2	11.8	8.7	30.8	
HCRP-FC863	Eurygnathohippus sp.	lt	m3	25.1	26.4	11.7	8.2		10.5	10.9		7.9		
HCRP-FC549	Eurygnathohippus sp.	rt	m3	26.3	26.4	11.6	8.0	12.2	10.1	10.4	9.9	10.1	42.1	
HCRP-FC613A	Eurygnathohippus sp.	lt	m3	İ		13.4	7.8	13.1		11.5	11.2	9.2	48.9?	
HCRP-FC554	Eurygnathohippus sp.	rt	P2			24.9	23.3	20.2	1	2	3	2	10.0	5.8
HCRP-FC559	Eurygnathohippus sp.	lt	P4	22.8	22.6	23.3	24.4	33.4	4	8	5	4	10.8	4.0
HCRP-FC815	Eurygnathohippus sp.	lt	P4	20.0	19.4	20.6	20.7	41.7	2	6	2	1	8.2	4.6
HCRP-FC853	Eurygnathohippus sp.	rt	P4	23.1	20.7	20.0	18.7?	53.5?		4	2	1	9.8	3.7
HCRP-FC854	Eurygnathohippus sp.	rt	P4	21.3	17.6	21.9	21.8	47.4	2	6	2	1	9.9	4.1
HCRP-FC528	Eurygnathohippus sp.	lt	M1	20.2	18.0	19.9	18.7	46.4	2	5	3	1	6.5	3.8
HCRP-FC812	Eurygnathohippus sp.	lt	M3	24.1	24.2	18.4	19.5	32.5	1	4	2	1	10.2	3.8
HCRP-FC525	Eurygnathohippus sp.	rt	M3			19.7	19.8	26.3		4		1	7.8	3.9
HCRP-FC607	Eurygnathohippus sp.	rt	M3	20.5	21.6	18.5	17.3	36.0	1	3	3	2	9.3	4.0
HCRP-FC817	Eurygnathohippus sp.	rt	M3	22.5	21.1	19.3		39.7	1	5	1	2	8.3	3.3
HCRP-FC855	Eurygnathohippus sp.	rt	M3	17??	22.7	15.9??	19.6	69.9					10.3??	
HCRP-FC564	Eurygnathohippus sp.	rt	M3	21.0	23.6	20.2?	23.1	41.9	2	6	2	1	10.0	