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THE LATEST MIOCENE HIPPARIONINE (EQUIDAE) FROM LEMUDONG'O, KENYA

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ABSTRACT

Four cheek teeth recovered from the latest Miocene Kenyan locality of Lemudong'o, Kenya, are described herein. All specimens are those of a medium-sized hipparion species, which is small for East African hipparions. The two lower cheek teeth demonstrate that these specimens are referable to the endemic African lineage, *Eurygnathohippus*. Comparison with other materials that have been studied by the author from Ethiopia, Kenya, and Tanzania suggest a referral to *Eurygnathohippus* cf. *feibeli* Bernor and Harris, 2003. Wear on a single upper cheek-tooth fragment suggests that the local *E.* cf. *feibeli* may not have been a dedicated grazer, but incorporated some browse into its diet. The fact that the entire hipparion sample from Lemudong'o is composed of cheek teeth, three out of four of which are fragmentary and appear to have been transported by fluviatile agencies, suggests that they are sampled from a distal taphonomic community. Given that *E. feibeli* is known to have had elongate, slender, distal limbs and was a cursorial form, one can hypothesize that the Lemudong'o hipparion inhabited open country habitats.

Introduction

Lemudong'o is a late Miocene mammalian-dominated fossil locality in the Narok District of Kenya, on the western margin of the Gregory Rift Valley. Vertebrate fossils derive from primarily two horizons within a continual sequence consisting of sands that fine upwards to a claystone and a re-worked tuff (Ambrose, Nyamai, et al., 2007). These sediments have excellent chronometric control based on a single-crystal argon age of just over 6 million years ago (Deino and Ambrose, 2007). More than 1,300 vertebrate fossils identifiable to family level have been recovered from this site since its discovery by scientists in 1994 (Ambrose, Hlusko, and Kyule, 2007). However, the equid fauna within this collection from Lemudong'o is sparse, and represents what would appear to be a single species of a smaller African hipparion. I report here on four cheek-tooth specimens attributable to the genus *Eurygnathohippus* Van Hoepen, 1930.

Materials and Methods

The nomen *Hipparion* has been applied in a variety of ways by different authors. A history of Old World hipparion systematics has been provided by Bernor et al. (1996), while the African record has been addressed by Bernor and Armour-Chelu (1999), Bernor and Harris (2003), and Bernor et al. (2005). The evolutionary relationships of African hipparions and Eurasian members of the "*Sivalhippus*" Complex (sensu Bernor and Hussain, 1985) was first noted by Bernor and Lipscomb (1995).

The Lemudong'o material available for study is limited to cheek teeth, as no other skeletal elements have been recovered to date. This allows basic morphological description following the methodology of Bernor et al. (1997) and Bernor and Harris (2003). In that these cheek teeth are rolled, very limited statistical analysis can be effectively undertaken. I provide a single bivariate plot of a p4 specimen's occlusal length (M1-occlusal maximum length) versus maximum width (M8, across metaconid-protoconid band). Here, as in the previous studies cited above, I produce a 95% confidence ellipse using the Eppelsheim (Germany, ca. 10 Ma) population sample, and plot late Miocene–early Pliocene specimens from the Middle Awash (Ethiopia) and Lothagam (Kenya) against these. This provides some very basic information about the Lemudong'o hipparion's relative size. There is no reason to believe that this small sample represents more than a single hipparion species.

All measurements are in millimeters (mm). Measurement numbers (i.e., M1, M2, M3, etc.) of cheek teeth used here, as well as anatomical nomenclature follows Bernor et al. (1997).

Systematic Paleontology

Class MAMMALIA Linnaeus, 1758
Order PERISSODACTYLA Owen, 1848
Suborder HIPPOMORPHA Wood, 1937
Superfamily EQUOIDEA Hay, 1902
Family EQUIDAE Gray, 1821

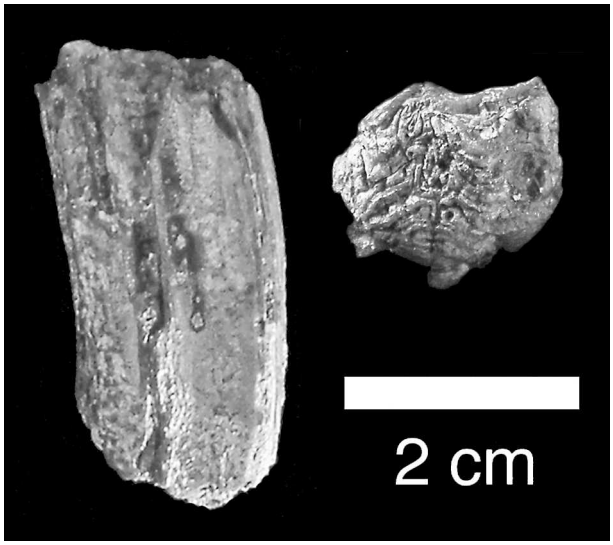

Figure 1. KNM-NK38312, right maxillary M3. Left, labial view; right, occlusal view.

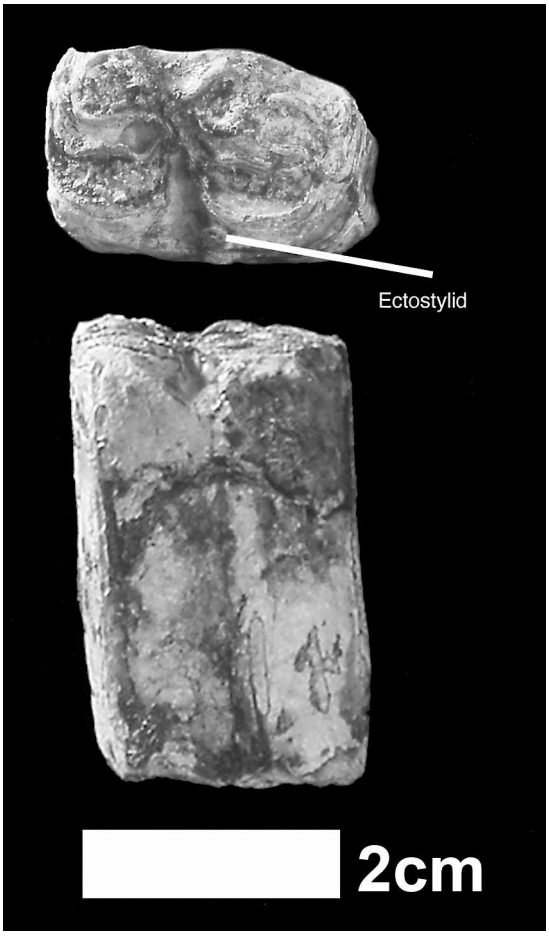

Figure 2. KNM-NK40994, left mandibular p4. Bottom, labial view; top, occlusal view.

Subfamily EQUINAE Steinmann and Doderlein, 1890
Genus *EURYGNATHOHIPPUS* Van Hoepen, 1930

Remarks

All African hipparions of the genus *Eurygnathohippus* are united by the synapomorphy of the presence of ectostylids on the permanent cheek teeth. Eurasian and North American hipparions do not have this character except very rarely in extremely worn hipparion teeth from the Dinotheriensandes, Germany (MN9, ca. 10.5–10 Ma). *Stylohipparion* is the junior synonym of *Eurygnathohippus* by year priority.

EURYGNATHOHIPPUS cf. *FEIBELI* Bernor and Harris, 2003
Figures 1–2

Type locality of *E. feibeli*

Upper Nawata Formation, Lothagam Hill, Kenya.

Geographic range

Ethiopia, Kenya, and possibly Tanzania.

Material

KNM-NK36935, left maxillary cheek-tooth fragment; KNM-NK38312, right maxillary M3; KNM-NK41375, right mandibular p4 fragment; KNM-NK40994, left mandibular p4.

Description

KNM-NK36935 is a central fragment of a left maxillary cheek tooth of a smaller East African hipparion. Here, most of the prefossette and all of the postfossette are preserved. The posterior border of the prefossette is complexly ornamented, as is the opposing border of the prefossette. There is a moderately deep groove across the middle of the tooth that would have extended from the lingual surface of the protocone to the labial border of the mesostyle (both missing in this specimen). This feature, characteristically deeper in most populations of *Hippotherium primigenium,* functionally correlates with rounded-to-sharp and high facets on the ectoloph, and is correlated with a mixed grass/browse to a browse diet (Kaiser et al., 2000). Given that this functional trough is shallow, we can only safely estimate that this individual did not likely have a purely grass diet: It likely browsed somewhat.

KNM-NK38312 (Figure 1) is a more complete, and small maxillary M3. The occlusal surface is eroded and appears to have been in relatively early wear. The pre- and postfossettes can be distinguished but are not yet sufficiently worn to have any developed plications. There is a single pli caballin and the protocone is rounded labially, and strongly flattened lingually. No other morphological features are clearly displayed on this apparently rolled specimen.

KNM-NK41375 is a fragmentary right mandibular p4 of a similarly sized hipparion. The mesial portion of the tooth is broken away. The following morphological features are preserved: a rounded metastylid with a straight sloping mesiolingual border; an elongate, unplicated postflexid; a shallow ectoflexid, not separating metaconid-metastylid; a distinct pli caballinid, and what appears to be a tiny ectostylid immediately labial to the pli caballinid.

KNM-NK40994, a complete mandibular p4, is the best preserved specimen in this sample (Figure 2). Its salient features include: rounded metaconid and square-shaped metastylid; linguaflexid a deep, broad U-shape*; preflexid and postflexid elongated, labiolingually compressed and lacking any plications*;

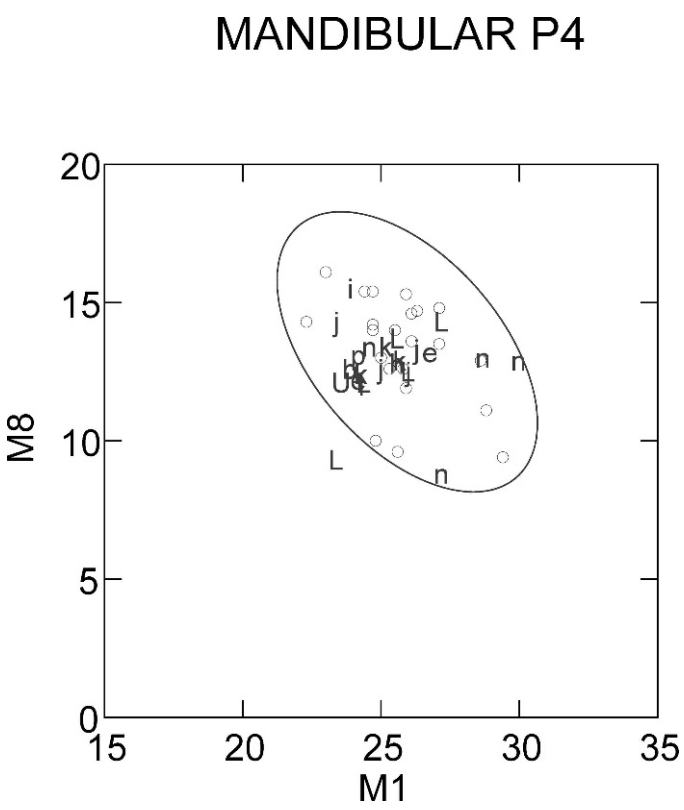

Figure 3. Bivariate plot of KNM-NK40994, left mandibular p4: M8 versus M1, 95% confidence ellipse representing variability in the Eppelsheim sample, 10 Ma., Germany.

protoconid enamel band showing some flattening*; ectoflexid not separating metaconid-metastylid; pli caballinid small; ectostylid a distinct, albeit small, elongate, enamel circle on the mid-labial margin of the tooth* (* indicates features typical of *Eurygnathohippus*). This was the only specimen for which measurements (Table 1) could be effectively made.

Haile-Selassie (2001) has recognized that it is difficult to distinguish the two lineages of late Miocene–medial Pliocene East African hipparions from cheek teeth alone: they are well characterized by distal postcranial elements (Bernor et al., 2005). This is exacerbated by the fact that cheek teeth reduce their mesiodistal dimension through wear, so that old individuals have much shorter dimensions than young individuals. Nevertheless, these studies have recognized a smaller hipparion during this time interval, and it is interesting that its cheek teeth are consistently the size of Central European late Miocene *Hippotherium primigenium*.

Figure 3 is a bivariate plot of KNM-NK40994 in comparison to the Eppelsheim sample (95% confidence ellipse and plotted points indicated by circles). The Lemudong'o specimen is indicated by a U and placed near the left border of the Eppelsheim ellipse. Lothagam (L) has specimens both inside the ellipse and further to the right (and hence are longer), as well as outside, lower and to the left of the ellipse (and hence being narrower). The remaining lower case indications (i, j, k, n, etc.) are latest Miocene-earliest Pliocene Middle Awash localities. In that these localities are not yet published, I will only note here that they are between 5.7 and 4.9 Ma, and are of the same species-lineage. The Lemudong'o specimen was in approximate middle wear, and its size is clearly that of Eppelsheim *Hippotherium primigenium*. Although fragmentary, all other specimens in the Lemudong'o hipparion are the size of this hipparion.

Remarks

Hipparionine horses originated in North America circa 16 Ma and first entered the Old World between 11.1 and 10.7 Ma. The Eurasian late Miocene record is extensive and includes several multispecies superspecific groups. Members of the major clades including *Hippotherium, Hipparion s.s.*, and *Cremohipparion* became extinct at the end of the late Miocene (Bernor et al., 1996). The "*Sivalhippus*" Complex is first recorded in the late Miocene of IndoPakistan and East Africa, and later had ranges that extended across Eurasia and Africa (Bernor and Lipscomb, 1995). The Chinese taxa *Plesiohipparion* and *Proboscidipparion* appear to have extended their ranges into Europe and southwest Asia in the early Pliocene (Bernor et al., 1996), while *Eurygnathohippus* was a vicariant lineage restricted to East and South Africa in the late Miocene (Bernor and Lipscomb, 1995; Bernor and Harris, 2003; Bernor et al. 2004), and is known throughout Africa during the Plio-Pleistocene (Bernor and Armour-Chelu, 1999).

Bernor et al. (2005) have analyzed Ethiopian hipparion metapodials and 1st phalanges between 6.0 and 2.9 Ma in age. They have found evidence of two hipparion lineages during this interval. A rare robust form, related to Lothagam *Eurygnathohippus turkanense*, and a predominant gracile lineage that they refer to the *Eurygnathohippus feibeli-hasumense* lineage. This lineage would appear to have progressively evolved greater size (= body mass) and to have lengthened the metapodials and increased the size of the phalanges from 6 to 2.9 Ma. The earliest members of this lineage are referable to *Eurygnathohippus feibeli s.s.*, and are the smallest members of this lineage. The Lemudong'o sample is similar to *E. feibeli*, and has all the morphological hallmarks of *E. feibeli*, but the absence of metapodial and 1st phalangeal material necessitates a referral to *E.* cf. *feibeli.*

Conclusions

The Lemudong'o hipparion sample is small for East African hipparions, and referable to *Eurygnathohippus* cf. *feibeli*. Referral to *Eurygnathohippus* is clearly supported by the occurrence of an ectostylid on at least one, and probably two permanent mandibular cheek teeth. The small size and morphology of this sample support the specific referral to *E.* cf. *feibeli*. Wear on the upper cheek tooth suggests that there may have been some component of browse in this sample. The Lemudong'o hipparion would appear to correlate well with Upper Nawata Formation (Bernor and Harris, 2003), Middle Awash latest Miocene hipparions (observations of myself and Y. Haile-Selassie) and the oldest Manonga Valley hipparion-bearing levels (Bernor and Armour-Chelu, 1997): all have this size hipparion, most likely referable to *E. feibeli*.

The fact that hipparions are so poorly represented at Lemudong'o, coupled with the fact that the specimens are largely fragmentary and appear to be transported by fluviatile agencies, suggests that they are sampled from a distal taphonomic community. *Eurygnathohippus feibeli* is known to have had elongate distal limb elements, and is believed to have lived in open country habitats. These lines of evidence support the observations elsewhere in this volume that Lemudong'o principally sampled a more closed ecological setting (i.e., the proximal taphonomic community), and that the hipparions sample a somewhat distant open country community (Ambrose, Bell, et al., 2007).

Table 1. Measurements on KNM-NK40994, left mandibular p4.

Measurement*	Description	KNM-NK 40994
M1	occlusal length	23.6
M3	metaconid-metastylid length	13.6
M4	preflexid length	8.1
M5	postflexid length	10.2
M8	width across plane of metaconid-protoconid enamel band	12.1
M9	width across plane of metastylid-hypoconid	11.1
M11	length of ectostylid	2.3
M12	width of ectostylid	1.2

*All measurements in mm.

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References

Ambrose, S. H., C. J. Bell, R. L. Bernor, J. R. Boisserie, C. M. Darwent, D. DeGusta, A. Deino, N. Garcia, Y. Haile-Selassie, J. J. Head, F. C. Howell, M. D. Kyule, F. K. Manthi, E. M. Mathu, C. M. Nyamai, H. Saegusa, T. A. Stidham, M. A. J. Williams, and L. J. Hlusko. 2007. The paleoecology and paleogeographic context of Lemudong'o Locality 1, a late Miocene terrestrial fossil site in southern Kenya. Kirtlandia, 56:38–52.

Ambrose, S. H., M. D. Kyule, and L. J. Hlusko. 2007. History of paleontological research in the Narok District of Kenya. Kirtlandia, 56:1–37.

Ambrose, S. H., C. Nyamai, E. Mathu, M. D. Kyule, and M. A. J. Williams. 2007. Geology, geochemistry, and stratigraphy of the Lemudong'o Formation, Kenya Rift Valley. Kirtlandia, 56:53–64.

Bernor, R. L., and M. Armour-Chelu. 1997. Later Neogene hipparions from the Manonga Valley, Tanzania, p. 219–264. *In* T. Harrison (ed.), Neogene Paleontology of the Manonga Valley, Tanzania, Topics in Geobiology Series. Plenum, New York.

Bernor, R. L., and M. Armour-Chelu. 1999. Toward an evolutionary history of African Hipparionine horses, p. 189–221. *In* T. Brommage and F. Schrenk (eds.), African Biogeography, Climate Change and Early Hominid Evolution. Wenner-Gren Foundation Conference, Livingstonia Beach Hotel, Salima, Malawi. Oxford.

Bernor, R. L., and J. M. Harris. 2003. Systematics and evolutionary biology of the late Miocene and early Pliocene hipparionine horses from Lothagam, Kenya, p. 387–438. *In* J. M. Harris and M. Leakey (eds.), Lothagam: The Dawn of Humanity in Eastern Africa. Columbia University Press, New York.

Bernor, R. L., and S. T. Hussain. 1985. An assessment of the systematic, phylogenetic and biogeographic relationships of Siwalik hipparionine horses. Journal of Vertebrate Paleontology, 5(1): 32–87.

Bernor, R. L., T. Kaiser, and S. V. Nelson. 2004. The oldest Ethiopian hipparion (Equinae, Perissodactyla) from Chorora: systematics, paleodiet and paleoclimate. Courier Forschungsinstitut Senckenberg, 246:213–226.

Bernor, R. L., G. D. Koufos, M. O. Woodburne, and M. Fortelius. 1996. The evolutionary history and biochronology of European and southwestern Asian late Miocene and Pliocene hipparionine horses, p. 307–338. *In* R. L. Bernor, V. Fahlbusch, and H.-W. Mittmann (eds.), The Evolution of Western Eurasian Later Neogene Faunas. Columbia University Press, New York.

Bernor, R. L., and D. Lipscomb. 1995. A consideration of Old World hipparionine horse phylogeny and global abiotic processes, p. 164–177. *In* E. S. Vrba, G. H. Denton, T. C. Partridge, and L. H. Burckle (eds.), Paleoclimate and Evolution, with Emphasis on Human Origins. Yale University Press, New Haven.

Bernor, R. L., R. Scott, and Y. Haile-Selassie. 2005. A contribution to the evolutionary history of Ethiopian hipparionine horses: morphometric evidence from the postcranial skeleton. Geodiversitas, 27(1): 133–158.

Bernor, R. L., H. Tobien, L.-A. Hayek, and H.-M. Mittmann. 1997. The Höwenegg hipparionine horses: systematics, stratigraphy, taphonomy and paleoenvironmental context. Andrias, 10:1–230.

Deino, A. L., and S. H. Ambrose. 2007. $^{40}Ar/^{39}Ar$ dating of the Lemudong'o late Miocene fossil assemblages, southern Kenya Rift. Kirtlandia, 56:65–71.

Gray, J. E. 1821. On the natural arrangement of vertebrose animals. London Medical Repository, 15(1): 296–310.

Haile-Selassie, Y. 2001. Late Miocene mammalian fauna from the Middle Awash Valley, Ethiopia. Unpublished Ph.D. dissertation, University of California, Berkeley. 425 p.

Hay, O. P. 1902. Bibliography and catalogue of the fossil Vertebrata of North America. U.S. Geological Survey Bulletin 179, 868 p.

Kaiser, T. M., N. Solounias, M. Fortelius, R. L. Bernor, and F. Schrenk. 2000. Tooth mesowear analysis on *Hippotherium primigenium* from the Vallesian Dinotheriensande (Germany): a blind test study. Carolinea, 58:103–114.

Owen, R. 1848. Description of teeth and portions of jaws of two extinct anthracotherioid quadrupeds...discovered in the Eocene deposits on the N. W. coast of the Isle of Wight. Quarterly Journal of the Geological Society of London, 4:103–141.

Steinmann, G., and L. Döderlein. 1890. Elemente der Paläontologie. Wilhelm Engelmann, Leipzig. 848 p.

Van Hoepen, E. C. N. 1930. Fossiele Pferde van Cornelia. O. V. S. Paleontologie Navorsing Nasionale Museum Bloemfontein, 2:13–24.

Wood, H. E. 1937. Perissodactyl suborders. Journal of Mammalogy, 18(1):106 p.