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Hooijer's Hypodigm for "*Hipparion*" cf. *ethiopicum* (Equidae, Hipparioninae) from Olduvai, Tanzania and comparative Material from the East African Plio-Pleistocene

by

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Abstract

We review here the problematic history of the nomen *"Hipparion"*cf. *ethiopicum* and Hooijer's efforts to bring some taxonomic sense to the later Pliocene – Pleistocene hipparion record. We review his reasoning, and the shifts in taxonomic allocation made by him and other equid researchers during the 1970's. We have relocated many of the postcranial specimens attributed by Hooijer to *"Hipparion"* cf. *ethiopicum,* as well as other specimens which he referred to, or related to this species. We have also considered additional specimens from contemporaneous horizons, in order to reevaluate the efficacy of *Eurygnathohippus* cf.*"ethiopicum"* and its apparent relative *Eurygnathohippus cornelianus,* and species believed by Hooijer to be evolutionarily related to *"Hipparion" ethiopicum*. We undertake statistical and comparative analyses to clarify these hypodigms.

Keywords: *Hipparion*, *Eurygnathohippus*, Olduvai, Omo, Plio-Pleistocene

Zusammenfassung

Wir beschäftigen uns hier mit der problematischen Geschichte des Taxons „*Hipparion*" cf. *ethiopicum* und Hooijers Bemühungen, eine taxonomische Stimmigkeit in die plio-/pleistozänen Hipparionen-Funde zu bringen. Wir folgen seinen Überlegungen und den taxonomischen Veränderungen die er und andere Equiden-Forscher während der 1970er-Jahre angestellt haben. Viele der postcranialen Elemente die Hooijer zu diesem Taxon gestellt hat, auf die er sich bezogen hat oder die in irgendeiner Beziehung dazu stehen, haben wir wiedergefunden. Selbst zusätzliche Fundstücke aus zeitgleichen Horizonten haben wir miteinbezogen, in der Absicht, die Gültigkeit von *Eurygnathohippus* cf.*"ethiopicum"* und seines Verwandten *Eurygnathohippus cornelianus* und weiterer Formen, von denen Hooijer geglaubt hat, dass sie in einem evolutionären Zusammenhang mit „*Hipparion*" cf. *ethiopicum* stehen, zu testen. Wir machen statistische und vergleichende Analysen um dieses Hypodigma zu klären.

1. Introduction

The genus *Eurygnathohippus* is distinctly African, first appearing in the Late Miocene and clearly related to the IndoPakistan genus *Sivalhippus* (sensu Bernor & Hussain, 1985; Bernor & Lipscomb, 1991, 1995). The lineage apparently became extinct sometime after 1.0 Ma and considering the great geographic extent of its pan-African range, realized relatively low species diversity compared to Eurasian hipparions. While there has been a plethora of African hipparion taxa erected, there are in fact relatively few bonafide taxa recognized (see Bernor & Armour-Chelu, 1999 for a review). The earliest reported representatives of the genus *Eurygnathohippus* are *E. turkanense* and *E. feibeli* from the lower member of the Nawata Formation, Lothagam, Kenya (Bernor & Harris, 2003), dating to 7.4 - 6.5 Ma (McDougall & Feibel, 2003). *Eurygnathohippus turkanense* was first described from Lothagam by Hooijer & Maglio (1973) as a large bodied hipparion lacking a preorbital fossa. *Eurygnathohippus turkanense* was considered by Hooijer & Maglio (1973, 1974) to be ancestral to *"Hipparion"* cf. *ethiopicum* (= *E. cornelianus*) which is a widespread and abundant taxon in East African localities dating to the Plio-Pleistocene. Hooijer's identification of *H.* cf. *ethiopicum* was largely based upon his observations of a series of dentitions from Olduvai and Laetoli, Tanzania, (Hooijer, 1975, 1979, 1987a). Hooijer characterized this lineage as exhibiting increased crown height and ectostylid development culminating in the advanced hipparion found in Bed II, Olduvai (Leakey, 1965).

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Locality	Reference	Element	Specimen-No.	Identification
Lothagam	Hooijer & Maglio, 1974	Astragalus	KNMLT-156	*H. turkanense*
Lothagam	Hooijer & Maglio, 1974	Astragalus	KNMLT-160	*H. turkanense*
Omo, C	Hooijer, 1975	Astragalus	L183-26	*H.* spec.
Omo, C	Hooijer, 1975	MT III	L46-34	*H.* spec.
Omo, F	Hooijer, 1975	MT III	L65-30	*H.* aff. *sitifense*
Omo, G	Hooijer, 1975	MT III	L892-7	*H. ethiopicum*
Omo, G	Hooijer, 1975	MT III	L48-7	*H. ethiopicum*
Omo, G	Hooijer, 1975	MT III	L596-22	*H. ethiopicum*
Omo, H	Hooijer, 1975	Astragalus	P955-I	*H. ethiopicum*
Olduvai, Bed I	Hooijer, 1975	MC III	FLKN 933	*H.* cf. *ethiopicum*
Olduvai, Bed I	Hooijer, 1975	MC III	FLKN 7693	*H.* cf. *ethiopicum*
Olduvai, Bed II	Hooijer, 1975	MC III	LGK 366	*H.* cf. *ethiopicum*
Olduvai, Bed II	Hooijer, 1975	MC III	SHK 576	*H.* cf. *ethiopicum*
Olduvai, Bed II	Hooijer, 1975	MC III	SHK 935	*H.* cf. *ethiopicum*
Olduvai, Bed II	Hooijer, 1975	MC III	BK 2750	*H.* cf. *ethiopicum*
Olduvai, Bed II	Hooijer, 1975	MC III	MNK SK 167	*H.* cf. *ethiopicum*
Olduvai Bed?	Hooijer, 1975	MC III	F45	*H.* cf. *ethiopicum*
Olduvai, Bed II	Hooijer, 1975	MT III	HWK S 86	*H.* cf. *ethiopicum*
Olduvai, Bed II	Hooijer, 1975	MT III	SHK 557	*H.* cf. *ethiopicum*
Olduvai, Bed II	Hooijer, 1975	MT III	SHK 728/730	*H.* cf. *ethiopicum*
Olduvai, Bed II	Hooijer, 1975	MT III	SHK 1177	*H.* cf. *ethiopicum*
Olduvai, Bed II	Hooijer, 1975	MT III	BK 68	*H.* cf. *ethiopicum*
Olduvai, Bed II	Hooijer, 1975	MT III	BK 135	*H.* cf. *ethiopicum*
Olduvai, Bed II	Hooijer, 1975	MT III	BK 620	*H.* cf. *ethiopicum*
Olduvai, Bed II	Hooijer, 1975	MT III	BK no num.	*H.* cf. *ethiopicum*

Table 1: Specimen identifications after Hooijer.

Further analyses of East African hipparion (Eisenmann, 1976b, 1983) have largely confirmed Hooijer's descriptions and conclusions, but the hypodigm for "*H*". cf. *ethiopicum* still remains problematic. In part this is due to incomplete analysis and description of postcranial specimens and the lack of associated cheek teeth and anterior dentitions. There further remains the outstanding issue of whether Hooijer's concept of "*H*" cf. *ethiopicum* contains a single, or multiple species (Eisenmann, 1983; Forsten, 1996; Bernor & Armour-Chelu, 1999). In this study we briefly review these taxonomic issues and present analyses of postcranial material assigned to "*H*". cf. *ethiopicum* by Hooijer, along with other East African hipparion material, in order to further characterize this taxon. Clearly, this taxonomic muddle can only be resolved by continued study and analysis of all relevant fossil materials. In this contribution, we attempt to analyze and further describe Hooijer's hypodigm *H.* cf. *ethiopicum* (= *E. cornelianus* but not necessarily *H. ethiopicum* from Omo Member F).

2. History of Hooijer's Investigations

The most common hipparion identified from East Africa between 2.5 and 1 Ma has been referred by many authors to *H. ethiopicum* or *H.* cf. *ethiopicum*. Both of these taxa are now known to be best referred to the genus, *Eurygnathohippus*, while the boundaries between the species nomina remain obscure. The earliest occurrence of this "lineage" appears to be from the Upper Ndolanya Beds, Laetolil, Tanzania, which are capped by the Ogol lavas dating to around 2.4 Ma. (Drake & Curtis, 1987). It is also identified in the Omo, Shungura F, dated to 2.36 Ma (Brown et al., 1985). However, the specific identification of hipparion remains from late Plio-Pleistocene levels in East Africa is confused by a rather tortured synonomy (*Hipparion* cf. *ethiopicum*, *Hipparion cornelianum*, *Stylohipparion* cf. *albertensis*, *Stylohipparion libycum* and *Libyhipparion ethiopicum*) and uncertainty regarding the number of taxa actually represented by these designations. In their review of this problem, Churcher & Richardson (1978) referred all Late Pliocene-Pleistocene African hipparions to a single species, *Hipparion libycum* suggesting that three regional subspecies be recognized: *Hipparion libycum libycum, Hipparion libycum ethiopicum, Hipparion libycum steytleri* for assemblages in North Africa, East Africa and South Africa, respectively. The problem with this taxonomic solution is threefold:

1. detailed morphological comparisons between all of these populations have not been made;
2. crucial statistical analysis of postcranial elements have not been made;
3. the diagnostic anterior premaxillary and mandibular dentitions are lacking in most Plio-Pleistocene African equid assemblages rendering species discrimination and referral very difficult.

Hipparion cf. *ethiopicum*	HOOIJER, 1975
Hipparion cf. *ethiopicum*	HOOIJER, 1979
Hipparion libycum ethiopicum	HOOIJER & CHURCHER, 1985
Hipparion cf. *ethiopicum*	EISENMANN, 1976a
Hipparion cornelianum	EISENMANN, 1983
Hipparion cf. *cornelianum*	EISENMANN, 1998
Hipparion libycum	CHURCHER & RICHARDSON, 1978
Eurygnathohippus "cornelianus"	This paper

Table 2: Synonyms for *Eurygnathohippus "cornelianus"*

In a series of publications, HOOIJER (1975, 1976, 1979, 1987a, 1987b) provided a detailed description of the skull and teeth of taxon that he variously referred to *H. ethiopicum*, *H.* cf. *ethiopicum* and *H. libycum ethiopicum*. Hooijer's apparently inconsistent nomenclature reflects the ambiguities surrounding the true identity of the advanced hipparion(s) found throughout East Africa during the Plio-Pleistocene. Hooijer recognized four hipparion taxa from the Omo deposits (ca. 4.5-1.0 Ma; HOOIJER, 1975, 1976; HOOIJER & CHURCHER, 1985), *Hipparion turkanense, H.* aff. *sitifense, H.* spec. and *H. ethiopicum*. *Eurygnathohippus turkanense* was identified by a single tooth from Yellow Sands, Mursi Formation dating to 4.5 Ma (BROWN et al., 1985). One species was identified from Omo Member C, as "*H*". spec. and HOOIJER (1975) suggested that it was part of an evolving population that included "*H*". *ethiopicum*. It was characterized as having fairly high crowned teeth but ectostylids not as developed as found in material from Member F. An astragalus and a distal portion of a metatarsal from Member C were also referred to this taxon. A more progressive form identified as *H. ethiopicum* (HOOIJER, 1975) is first recognized from Shungura Member F, dated to 2.36 Ma (BROWN et al., 1985).

In this assemblage HOOIJER (1975) acknowledged JOLEAUD's (1933) type material described from a collection of teeth recovered from the Omo. JOLEAUD (1933) actually referred his material to *Libyhipparion ethiopicum* but this designation was only followed in part by HOOIJER & MAGLIO (1973) who pointed out that if a new generic name was required, then *Eurygnathohippus* VAN HOEPEN 1930 should have priority. This taxonomic convention has since been adopted by BERNOR & LIPSCOMB (1991, 1995), BERNOR & ARMOUR-CHELU (1999), BERNOR & HARRIS (2003) and BERNOR et al. (2004, 2005). The type series for Joleaud's "*Libyhipparion*" *ethiopicum* is comprised of 12 teeth, of unknown stratigraphic provenance and homogeneity, within the Omo sequence. HOOIJER (1975) designated a lectotype for his concept of "*H*". *ethiopicum* by selecting a lower third molar from Joleaud's type series of *Libyhipparion ethiopicum*. EISENMANN (1983) has observed that this assemblage includes more than one species, and since no single type specimen was identified by Joleaud, the species nomen "*ethiopicum*" is of dubious value.

HOOIJER (1975) identified a second taxon from Member F as "*Hipparion*" aff. *sitifense* largely on the basis of the diminutive size of the teeth. "*Hipparion*" *sitifense* was originally named by POMEL (1897) for two teeth and a metapodial from the St. Arnaud Cemetery site, Algeria, which is believed to be Late Miocene or Early Pliocene age. Several authors have discussed the status of the North African form (EISENMANN, 1983; BERNOR & HARRIS, 2003; BERNOR & SCOTT, 2003) and have commented that the nomen has been inappropriately applied to East African small hipparions for a number of reasons including: 1. the type material has been lost, or at least has not been relocated in Paris (EISENMANN, pers. commun.); 2. there is no evidence that the lower cheek teeth of this form had ectostylids, which small East African hipparions usually have (albeit small and not rising on the side of the crown in the oldest and most primitive forms); 3. the principal diagnostic character for "*H*". *sitifense* is its small size, which can be ascribed just as easily to multiple species of *Cremohipparion,* including several specimens from the latest Miocene locality of Sahabi, Libya (BERNOR et al., 1996; BERNOR & SCOTT, 2003). BERNOR & HARRIS (2003) elected to rename Lothagam material previously assigned to "*H*". cf. *sitifense* to a new taxon *Eurygnathohippus feibeli* based on good, diagnostic postcranial material. This species has since been identified in the Middle Awash late Miocene sequence by BERNOR et al. (2005) and BERNOR & HAILE-SELASSIE (in press).

Fieldwork at Olduvai Gorge has produced a large assemblage of hipparion remains which were originally described by HOPWOOD (1937) and attributed to "*Stylohipparion*" cf. *albertensis*. The discovery of a skull in 1963 (BK, 2845/2846) from Upper Bed II, Olduvai, dating approximately 1.2 Ma helped clarify the identity of the Olduvai hipparion (HOOIJER, 1975: plate 7). HOOIJER (1975) noted similarities in the dentition and absence of preorbital fossa, among other features that phylogenetically related, for him, the skull to the Lothagam Lower Nawata species "*H*". *turkanense*. Louis LEAKEY (1958, 1965) also documented the similarity between the maxillary and mandibular anterior dentitions from the upper Bed II Olduvai and the type specimen of *Eurygnathohippus cornelianus*, a mandibular symphysis with incisors, from Uitsoek, near Cornelia, South Africa dating between 1.0 and 0.6 Ma (MCKEE et al., 1995; VRBA, pers. commun.), first described by VAN HOEPEN (1930).

The conspecificity between the anterior dentitions from Upper Bed II (BK site) and the mandibular symphysis from Uitsoek remains unchallenged. However, HOOIJER (1975) chose to refer all Olduvai hipparion teeth to a single taxon, "*H*". cf. *ethiopicum* and reserved the nomen "*H*". *ethiopicum* for material recovered from Member F and up, Omo (HOOIJER 1975). It is puzzling that Hooijer did not adopt the genus *Eurynathohippus* given the uniqueness of large ectostylids on the permanent mandibular cheek teeth and the evolution of extreme hypsodonty in this lineage.

HOOIJER (1979, 1987a, 1987b) also studied the hipparion from the Laetoli locality, which lies some 80 kilometers south of Olduvai. Laetoli samples deposits of disparate age. The Laetoli Beds date between 4.5 and 3.4 Ma whilst the

Locality	Identification	Specimen	Element	Citation
Lothagam	*E. turkanense*	KNM-LT 22871	MC III	Bernor & Harris, 2003
Lothagam	*E. turkanense*	KNM-LT 6088	Astragalus	Bernor & Harris, 2003
Lothagam	*E. turkanense*	KNM-LT 15667	Astragalus	Bernor & Harris, 2003
Lothagam	*E. turkanense*	KNM-LT 25433	Astragalus	Bernor & Harris, 2003
Lothagam	*E. turkanense*	KNM-LT 25470	MT III	Bernor & Harris, 2003
Omo, K	indet.	P996-8	Astragalus	This study
Olduvai, Bed II	*E. cornelianus*	KK 487	MC III	This study
Olduvai, Bed II	*E. cornelianus*	SWK 680	MC III	This study
Olduvai, Bed II	*E. cornelianus*	M16985	MC III	This study
Olduvai, Bed?	*E. cornelianus*	M14367	MC III	This study
Olduvai, Bed II	*E. cornelianus*	SHK 166	Astragalus	This study
Olduvai, Bed II	*E. cornelianus*	SHK 336	Astragalus	This study
Olduvai, Bed II	*E. cornelianus*	MNK 745	Astragalus	This study
Olduvai, Bed II	*E. cornelianus*	F780	Astragalus	This study
Olduvai, Bed I	*E. cornelianus*	M14363	MT III	This study
Olduvai, Bed II	*E. cornelianus*	DC 679	MT III	This study
Olduvai, Bed II	*E. cornelianus*	MRC 592	MT III	This study
Olduvai, Bed II	*E. cornelianus*	BK 1962	MT III	This study
Olduvai, Bed I	*E. cornelianus*	M14363	MT III	This study
Olduvai, Bed II	*E. cornelianus*	M16982	MT III	This study
Olduvai, Bed II	*E. cornelianus*	M16984	MT III	This study
Olduvai, Bed II	*E. cornelianus*	No acc. no.	MT III	This study
Olduvai, Bed III	*E. cornelianus*	M16983	MT III	This study
Olduvai, Bed?	*E. cornelianus*	M14366a	MT III	This study
Olduvai, Bed?	*E. cornelianus*	F797	MT III	This study
Laetoli, U. Ndolanya	*E.* aff. *cornelianus*	976/00a	MC III	This study
Laetoli, U. Ndolanya	*E.* aff. *cornelianus*	976/00b	MC III	This study
Laetoli, U. Ndolanya	*E.* aff. *cornelianus*	833/04 (7E)	Astragalus	This study
Laetoli, U. Ndolanya	*E.* aff. *cornelianus*	75-959	Astragalus	This study
Laetoli, U. Ndolanya	*E.* aff. *cornelianus*	75-787	Astragalus	This study
Laetoli, U. Ndolanya	*E.* aff. *cornelianus*	76-18-55	Astragalus	This study
Laetoli, U. Ndolanya	*E.* aff. *cornelianus*	75-2471 (14)	MT III	This study
Laetoli, U. Ndolanya	*E.* aff. *cornelianus*	75-903 (7E)	MT III	This study
Laetoli, U. Ndolanya	*E.* aff. *cornelianus*	75-904 (7E)	MT III	This study
Laetoli, U. Ndolanya	*E.* aff. *cornelianus*	76-18-153	MT III	This study
Laetoli, U. Ndolanya	*E.* aff. *cornelianus*	76-18-284	MT III	This study
Laetoli, U. Ndolanya	*E.* aff. *cornelianus*	1515/01 SA	MT III	This study

Table 3: Additional specimens of *Eurygnathohippus* mentioned in this paper.

Upper Ndolanya Beds are later, 2.7 - 2.4 Ma (Harrison, pers. commun.). In his original publication on the Laetoli hipparions Hooijer (1979) concluded that the material from the Upper Ndolanya Beds (2.7 - 2.4 Ma.) could be assigned to *H.* cf. *ethiopicum,* but later he revised his diagnosis and proposed that the advanced hipparion from Laetoli, Omo Member F (2.36 Ma) and Olduvai (1.9 - 1.0 Ma) were the same taxon (Hooijer & Churcher, 1985; Hooijer 1987b). It seems that by 1985 Hooijer had been persuaded by Churcher (Churcher & Richardson, 1978) that he should apply the nomen "*H.*" *libycum* Pomel 1897 in lieu of "*H.*" *ethiopicum* and that *Eurygnathohippus cornelianus* be suppressed. The implication is, of course, that "*H.*" *libycum* so applied is a taxon that geographically ranges from North Africa to Tanzania from the middle Pliocene – early Pleistocene. In our opinion, there is very little in the way of convincing morphological evidence to support this assertion, because over this time and space maximum crown heights varied, they clearly evolved through time in East Africa, and the all too critical anterior dentitions are infrequently recorded at localities other than Olduvai and in Cornelia. The only one of these taxa with a clear, cohesive morphological basis is *Eurygnathohippus cornelianus.* Gilbert & Bernor (in press) have found in their studies of the 1 Ma. Daka hipparion, that it can be related to both Olduvai Bed I and Bed II hipparion cheek teeth, metapodials and astragali, and is cogently referable to *E.* cf. *cornelianus,* despite the fact that the Daka assemblage does not include any complete premaxillary or mandibular incisor dentitions. In fact, the anterior

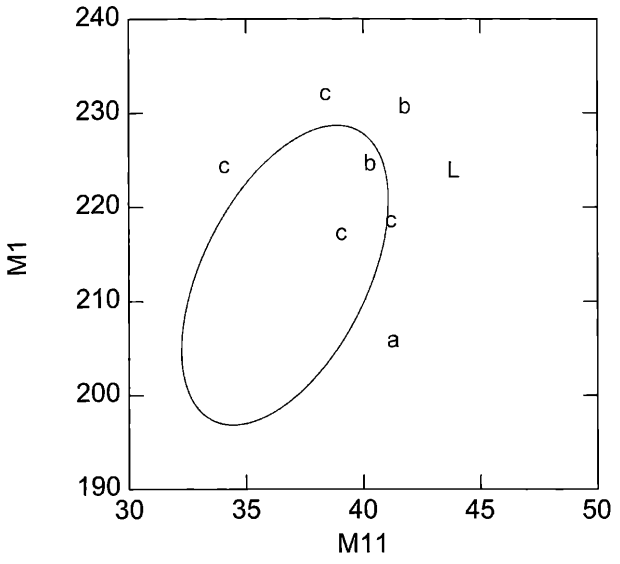

Figure 1: Hipparion Metacarpal III's from Olduvai, maximum length (M1) versus distal articular width (M11). Specimens identified by HOOIJER (1975) and specimen of *E. turkanense* from Lothagam (L) identified by authors added for size comparison.

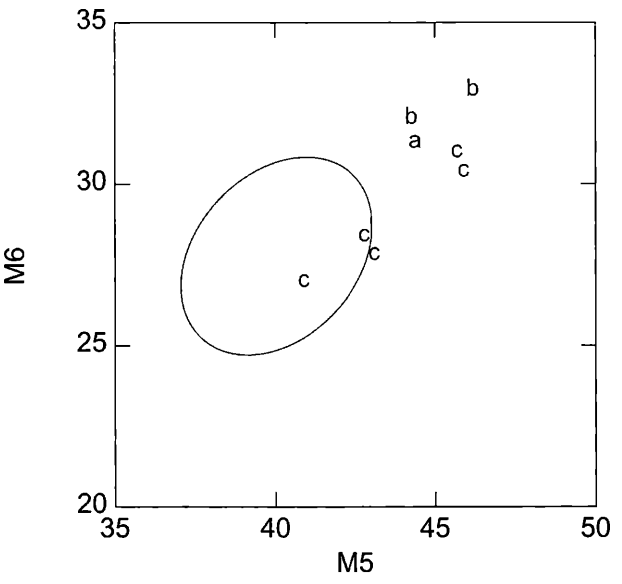

Figure 2: Hipparion Metacarpal III's from Olduvai, proximal articular depth (M6) versus proximal articular width (M5).

dentitions, including mandibular symphysis, premaxilla, incisors and canines are so distinctive in *E. cornelianus,* that there should be no confusion about its specific referral. What is needed is more hipparion incisor material, and in particular I3/i3's.

The taxonomy of *Eurygnathohippus "ethiopicum"* is further complicated by EISENMANN's (1983) and our own (BERNOR & ARMOUR-CHELU, 1999 and current studies) that there may be a second, albeit rare smaller, more gracile species of hipparion at Olduvai, as our plots of MTIII (Fig. 6) show here. There needs to be more material of this rare morph collected before we will be able to resolve its systematics and relationship to *Eurygnathohippus* cf *"ethiopicum"*.

3. Materials and Methods

Specimens analyzed here are housed in the National Natural History Museum, Naturalis, Leiden, The Netherlands (RMNH), The National Musem of Kenya, Nairobi, Kenya (KNM-LT designation for Lothagam), The National Museum, Dar-es-Salaam, Tanzania (LAET designation for Laetoli) and The Natural History Museum, London, U.K. (BMNH).

Measurements definitions and protocol follow EISENMANN et al. (1988) and BERNOR et al. (1997). All measurements are taken in mm, to the nearest tenth mm. We confine our analysis in this study to a series of bivariate plots using the skeletal population of *Hippotherium primigenium* from Höwenegg (Hegau, southern Germany, 10.3 Ma; BERNOR et al., 1997) for calculating 95% confidence ellipses used in bivariate plots. The Höwenegg standard is the only one we know of that includes several complete and partial articulated skeletons of a single species. As such, it provides us with robust statistics on the expected range of variability in standard bivariate measures. Recent applications of this methodology on African hipparions include studies of the Late Miocene – Early Pliocene Lothagam hipparion (ca. 7.4-5 Ma; BERNOR & HARRIS, 2003), terminal Miocene Sahabi hipparion (ca. 6.7 Ma; BERNOR & SCOTT, 2003), Late Miocene – medial Pliocene Middle Awash, late Early Pleistocene Daka (1 Ma, Ethiopia; GILBERT & BERNOR, in press) hipparion and Late Miocene Middle Awash (5.8 - 5.2 Ma; BERNOR & HAILE-SELASSIE, in press) hipparion. This work follows, and builds further upon BERNOR & ARMOUR-CHELU's (1999) review of taxonomic problems surrounding African hipparion taxonomy and evolution. Concurrent with this study is the study of Middle Awash (Ethiopia), Laetoli (Tanzania) and Langebaanweg (South African) hipparions which will be completed in the near future.

Definitions and Abbreviations:

Hipparionine or hipparion: horses with an isolated protocone on maxillary premolar and molar teeth and, as far as known, tridactyl feet, including species of the following genera: *Cormohipparion, Neohipparion, Nannippus, Pseudhipparion, Hippotherium, Cremohipparion, Hipparion,"Sivalhippus", Eurygnathohippus, Proboscidipparion,* and *Plesiohipparion.* Characterizations of these taxa have been most recently reviewed by BERNOR & ARMOUR-CHELU (1997, 1999) and BERNOR et al. (1996, 2005).

The osteological nomenclature and the enumeration and/or lettering of the figures have been adapted from NICKEL et al. (1986). GETTY (1982) was also consulted for morphological identification and comparison. Many figures present plots with abbreviations for different taxa and fossil samples. Olduvai hipparion are designated by lower case numbers as follows:

a = unknown stratigraphic horizon
b = Bed I provenience
c = Bed II provenience
d = Bed III provenience

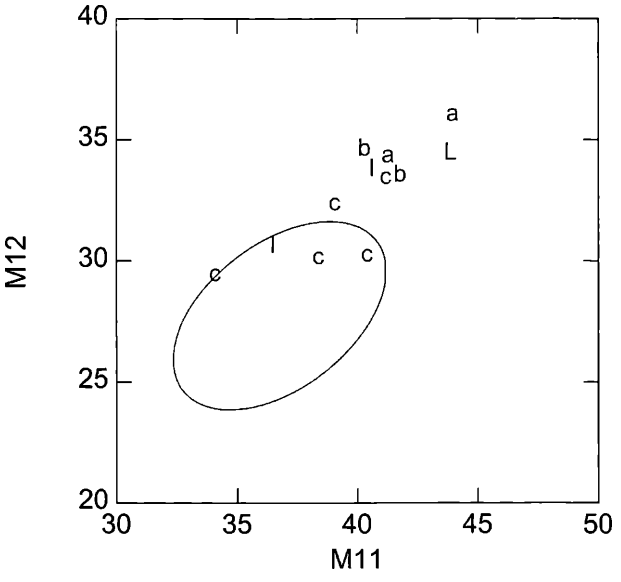

Figure 3: Hipparion Metacarpal III's from Olduvai, distal sagittal depth (M12) versus distal articular width (M11), with specimens of *E. turkanense* from Lothagam (L) and *E.* aff. *cornelianus* from Laetoli (I) for comparison.

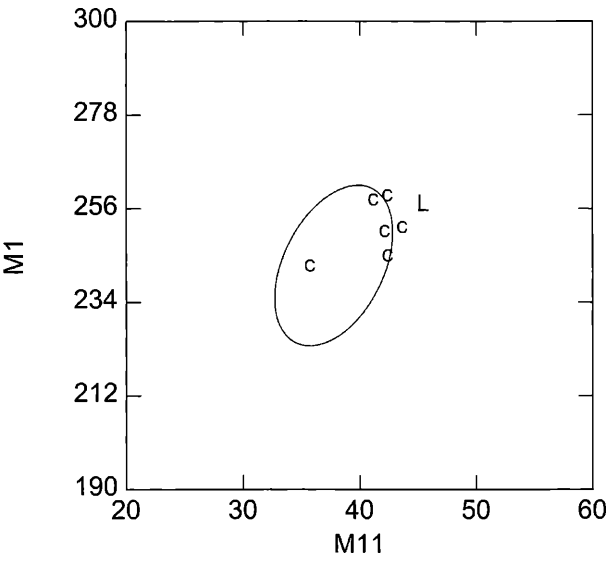

Figure 4: Hipparion Metatarsal III's from Olduvai, maximum length (M1) versus distal articular width (M11) including a single specimen of *E. turkanense* from Lothagam (L) (BERNOR & HARRIS, 2003).

Laetoli hipparion are designated by an upper case I.
Lothagam equids are designated by an upper case L.
Omo Shungura hipparion are designated by upper case C, F, G and K following their member provenience.
MC III – Metacarpal of the third (central) digit
MT III – Metatarsal of the third (central) digit

4. Analysis

Table 1 provides a list of specimens identified by HOOIJER (1975) from Lothagam, Omo Shungura C, F, G and H and Olduvai Beds I and II that are relevant to the allocation of material to his concept of *H.* cf. *ethiopicum*, and later, *H. libycum* (sensu HOOIJER & CHURCHER, 1985). Table 2 provides a list of taxonomic synonyms for *Eurygnathohippus "cornelianus"* and Table 3 identifies additional specimens identified, measured and analyzed here from Lothagam, Laetoli, Omo and Olduvai. HOOIJER (1975) identified ten MC III's and ten MT III's of "*H*". cf. *ethiopicum* from Beds I and II, Olduvai. Of these, we have relocated eight MC III's and eight MT III's. Two of these MC III's derive from Bed I and the remainder of the specimens are from Bed II, with the exception of one MC III, (RMNHF45), whose exact provenience is unknown.

Figures 1-4 are plots of different bivariate combinations for MC III. All specimens have been remeasured by us for statistical consistency.

Figure 1 includes Olduvai specimens of unknown provenience (a) and Bed I (b) and Bed II (c) plotted against the Höwenegg standard. The distribution of specimens is greater than what we would expect in a single species of hipparion. The "a" specimen, (RMNHF45), is markedly short and broad and exhibits morphology other than *E. cornelianus* (sensu GILBERT & BERNOR, in press). The Bed II individuals also seem to be scattered beyond what we expect for a single species, with two specimens being relatively elongate and slender (to the left of the ellipse) and two specimens plotting along the upper right margin of the ellipse. The Bed I individuals are at the top and outside the top right of the ellipse. The Bed I and Bed II distribution suggests at least two taxa, with the unprovenienced specimen most likely being a third taxon (RMNHF45). Also included in this figure is a complete MC III (L) reported by BERNOR & HARRIS (2003) from Lothagam as *Eurygnathohippus turkanense*. Its size and proportions are relatively massive compared to the Olduvai specimens reported here.

Figure 2 provides a plot of proximal articular depth (M6) versus proximal articular width (M5) of MC III from Olduvai Bed I, Bed II and unprovenanced specimens. There is one scatter of Bed II specimens on the right side of the Höwenegg ellipse, and another of Bed I and Bed II specimens, and a single unprovenanced specimen well above the ellipse exhibiting elevated proximal articular dimensions; these are substantially larger individuals than the Höwenegg hipparion.

Figure 3 is a plot of MC III distal sagittal keel depth (M12) versus distal articular width (M11). Two Bed II specimens plot within the Höwenegg ellipse, another just above the upper border of the ellipse, and a fourth in a cluster with two Bed I and a single unprovenienced specimen. Those specimens plotting above the ellipse evolved greater sagittal keel dimensions believed to be indicative of a shift to greater functional monodactyly during cursorial locomotion (BERNOR & SCOTT, 2003). This plot includes two individuals from Laetoli (I) and a specimen of *Eurygnathohippus turkanense* (L) from Lothagam. Of the two Laetoli specimens, one plots in the upper left quadrant of the Höwenegg ellipse, and the other plots within the Olduvai cluster. The results of this analysis suggest the following:
1. the hipparions plotted here had evolved greater distal

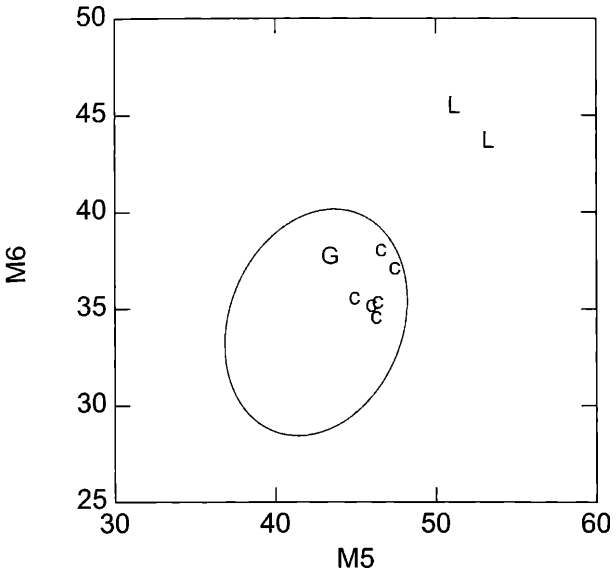

Figure 5: Hipparion Metatarsal III's, distal articular depth (M6) versus proximal articular width (M5) specimens identified by Hooijer from Olduvai (*H.* cf. *ethiopicum*) and Omo Shungura G (G = *H. ethiopicum* of HOOIJER, 1975) and two specimens of *E. turkanense* (BERNOR & HARRIS, 2003).

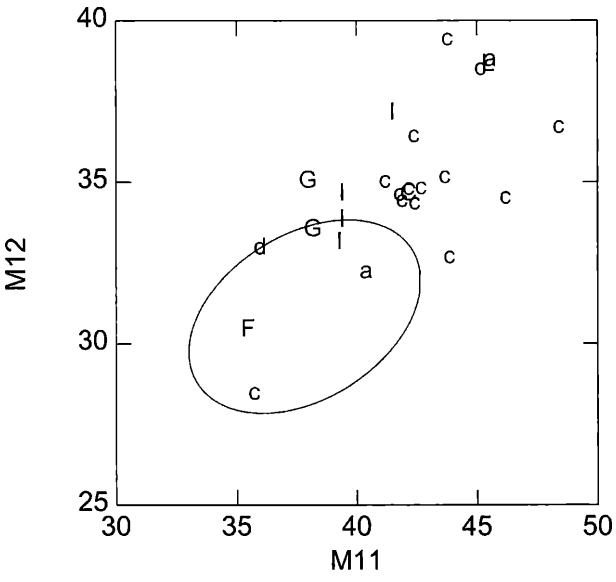

Figure 6: Hipparion Metatarsal III's from Olduvai, distal sagittal depth (M12) versus distal articular width (M11), including specimens from Omo Shungura F (*H.* aff. *sitifense*) and G (= *H. ethiopicum* of HOOIJER 1975) *E. turkanense* (L) from Lothagam, and *E.* aff. *cornelianus* from Laetoli (I) identified by the current authors.

sagittal keel diameter than the Höwenegg hipparion; 2. the hipparion from Laetoli (Upper Ndolanya) plots clearly with the Olduvai sample; 3. Lothagam *Eurygnathohippus turkanense* is a large, robustly built taxon with little similarity to *Eurygnathohippus cornelianus*.

Figure 4 is a plot of MT III maximum length (M1) versus distal articular width (M11) of six Bed II specimens. The range of variability is not greater than defined for the Höwenegg hipparion, but the sample does not cluster together either. One individual is both the shortest and narrowest of the sample (HWK S 86). Figure 4 plots an MT III of *Eurygnathohippus turkanense* (BERNOR & HARRIS, 2003), again showing the relative massiveness of the Lothagam species.

Figure 5 is a plot of MT III proximal articular depth (M6) versus proximal articular width (M5). It shows that all six Bed II specimens plotted fall within the upper right quadrant of the Höwenegg ellipse. A single Omo Shungura G specimen, (L892-7), likewise falls within this ellipse. The proximal MT III's considered here from Olduvai and Omo Shungura G are very similar in size and could belong to a single species. Two specimens referable to *Eurygnathohippus turkanense*, are much larger, particularly in the M6 dimension.

Figure 6 is a plot of MT III distal sagittal keel depth (M12) versus distal articular width (M11). HOOIJER (1975) identified the Bed II (c) specimens as being referable to *H.* cf. *ethiopicum*, the two Omo G specimens (L596-22, L48-7), to *Hipparion ethiopicum* and the Omo F specimen, (L65-30), to *Hipparion* aff. *sitifense*. Specimens from Laetoli, (Upper Ndolanya Beds), and Lothagam *Eurygnathohippus turkanense* are included for comparison. The Bed II specimen (HWK S 86) in the lowermost portion of the ellipse is strikingly smaller than the other Bed II specimens and even smaller than the small specimen from Omo F referred to *Hipparion* aff. *sitifense*. We believe that this is evidence of a rare, smaller second species of hipparion from Bed II Olduvai.

SCOTT et al. (2005) and GILBERT & BERNOR (in press) have recently demonstrated that astragali can be very useful for equid species distinctions. Figure 7 is a plot of astragali maximum length (M1) versus distal articular width (M5). A single specimen from Omo Shungura C plots in the upper portion of the ellipse, while a single specimen from Omo Shungura H plots below the ellipse. HOOIJER (1975) referred the Omo C specimen to *H.* spec, and the Omo H specimen to *H. ethiopicum*. A single specimen from Laetoli, two unprovenienced specimens from Olduvai, two specimens from Bed II and a single specimen from Bed III, Olduvai, and three specimens from the Lothagam Nawata are also plotted here. Again, the Omo Shungura H specimen clearly plots as a species smaller than the *E.* cf. *cornelianus* concept. The Olduvai specimens are similar in length to the Laetoli and Omo C specimens, but have broader distal articular surfaces. The Lothagam specimens include two individuals that are larger than all the rest, and referable to *E. turkanense*, and a third specimen that is not so long, but broader than the Olduvai, Laetoli and Omo specimens. This result suggests the following: the Omo Shungura H specimen should be referable to a species of *Eurygnathohippus* smaller than *E. cornelianus* and *E.* aff. *cornelianus*; the Olduvai specimens have astragali that are of similar length, but somewhat greater breadth than the Höwenegg sample; the Omo Shungura C and Laetoli astragali are the same fundamental size as the Höwenegg sample; the Lothagam sample, for the most part, belongs to a relatively large and massive hipparion species.

Figure 8 is a plot of astragali distal articular depth (M6)

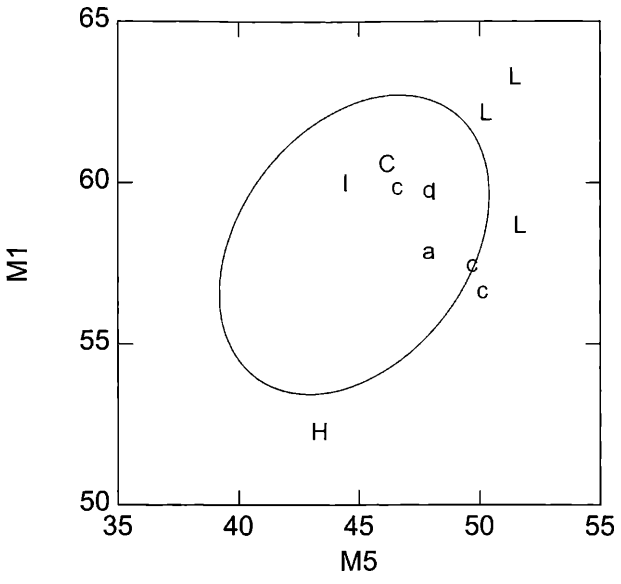

Figure 7: Hipparion astragali, from the Omo, maximum length (M1) versus proximal articular width (M5), specimens identified from Omo Shungura C (*H.* sp.) and H (*H. ethiopicum*) and three specimens of *E. turkanense* (BERNOR & HARRIS, 2003) and Olduvai added for comparison.

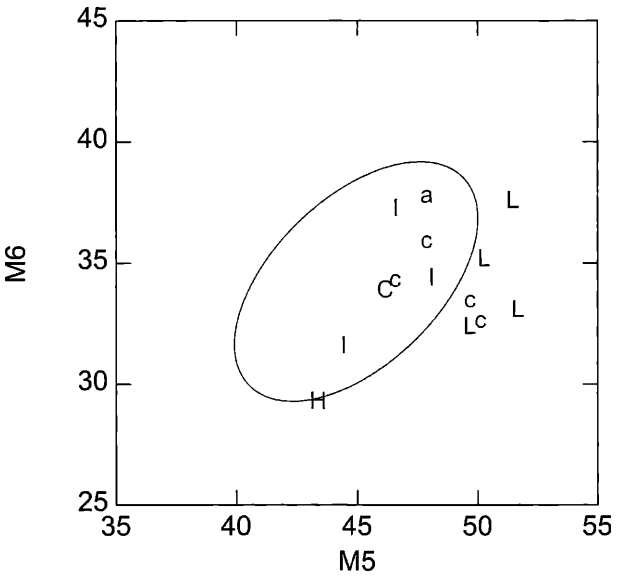

Figure 8: Hipparion astragali, from the Omo, proximal articular depth (M6) versus proximal articular width (M5), specimens identified by Hooijer from Omo Shungura C (*H.* sp.) and H (*H. ethiopicum*) and four specimens of *E. turkanense* (BERNOR & HARRIS, 2003), Laetoli *E.* aff. *cornelianus* and Olduvai hipparion specimens added for comparison.

versus distal articular width (M5). The plot is similar to Figure 7 of a Höwenegg sized specimen from Omo Shungura C and a smaller sized specimen from Omo Shungura H (P955-1). In this plot we have assembled additional data from Olduvai, Laetoli (Upper Ndolanya Beds) and the Lothagam Nawata Beds. Olduvai unprovenanced specimens as well as Bed II specimens both plot in the upper right portion of the Höwenegg ellipse and outside the upper right margin of the ellipse. They could represent a single species with greater mean width dimensions than the Höwenegg hipparion; they could also represent two separate taxa one of which could even be a smaller *Equus*. The three Laetoli specimens plot within the ellipse. The Lothagam specimens all plot to the right of the Höwenegg ellipse and overlap with three large Olduvai specimens in their distal articular width.

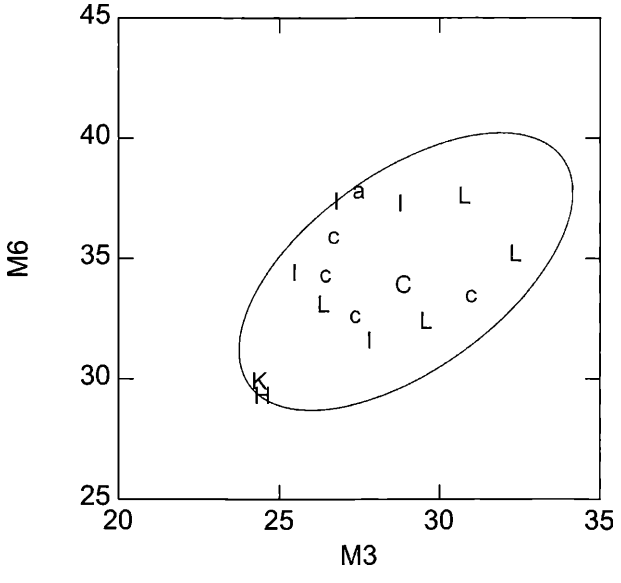

Figure 9: Hipparion astragali, from the Omo, (Shungura C - H. spec., H - *H. ethiopicum*, K (indet.), distal articular depth (M6) versus intra-trochlear width (M3) with specimens of *E. turkanense* (BERNOR & HARRIS, 2003), Laetoli *E.* aff. *cornelianus*, and Olduvai hipparion specimens added for comparison.

Figure 9 is a plot of astragali distal articular depth (M6) versus intra-trochlear width (M3) from Olduvai, (unprovenanced and Bed II), Laetoli (Upper Ndolanya Beds), Lothagam Nawata and Omo Shungura C, H and K. The same relationships for the Omo Shungura C and H apply from Figures 7 and 8. The wide range of variability for M3 expands the ellipse considerably. However, the most prominent feature again is the small size of the Omo Shungura H. A small equid astragalus from Omo Shungura K (P996-8) which remains unidentified is also included here. It plots with the astragalus from Omo Shungura H and thus would also be part of Hooijer's concept of "*Hipparion*" *ethiopicum*.

5. Conclusions

Our analyses suggest that most, but not all of the specimens considered here from Olduvai Beds I and II are referable to *Eurygnathohippus cornelianus* s.s., which is related, at least in part, to Hooijer's hypodigm of *H.* cf. *ethiopicum*. Material from the Upper Ndolanya Beds, Laetoli, plots with most of the Olduvai, Bed II sample and Omo Shungura G metatarsals may also derive from the same lineage as the Olduvai hipparion.

It seems likely that there is a small species of *Eurygnathohippus*, not referable to *E. cornelianus*, ("*Hipparion*"cf. *ethiopicum* of HOOIJER 1975), from Omo Shungura F, H, K

and Bed II Olduvai. This is represented by the two equid astragali from the Omo and two metatarsals from the Omo and Olduvai. There is also a large equid from Bed II similar in size to the Lothagam *E. turkanense* and this is either at the upper part of the range for *E. cornelianus* / *E.* aff. *cornelianus* or in fact a larger equid species. It is clear to us that there is more than a single sized taxon in Hooijer's concept of "*Hipparion*" cf. *ethiopicum*.

We continue to adopt here the convention recommended by BERNOR & ARMOUR-CHELU (1999) of provisionally recognizing the nomen *Eurygnathohippus "ethiopicus"* for some Omo Shungura F, G, and H hipparions. We believe that it is possible that the older *Eurygnathohippus "ethiopicus"* evolved its highly derived anterior dental morphology between 2.5 and 1.2 Ma. The phylogenetic history of this extremely derived, hypsodont short grass feeder is a fascinating example of adaptation and evolution that will likely be tied to the expansion of East and South African grassland communities (BERNOR & ARMOUR-CHELU, 1999).

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