Chapter 12
Equidae

Miranda Armour-Chelu and Raymond L. Bernor

Abstract Equid teeth and postcrania from the Laetolil and Upper Ndolanya Beds are described and compared with other hipparion assemblages from East and South African Plio-Pleistocene localities. The hipparion from the Laetolil Beds is morphologically similar to *Eurygnathohippus hasumense* from Hadar, although of slightly smaller dimensions, and is referred to *Eurygnathohippus* aff. *hasumense.* The hipparion from the Upper Ndolanya Beds closely resembles the advanced hypsodont form found at Olduvai Gorge (Bed I-IV), and is referred to *Eurynathohippus* aff. *cornelianus*.

Keywords *Eurygnathohippus hasumense* • *Eurygnathohippus cornelianus* • Hipparion • Equid • Ectostylid • Metacarpal III • Metatarsal III • Phalanx • Pliocene • Laetoli • Olduvai Gorge

Introduction

Mary and Louis Leakey first collected fossils from Laetoli in 1935 (Leakey 1987), in the area that later became known as Localities 10, 10W and 10E, from sediments dated to between 3.6 and 3.8 Ma. The fauna included hipparion remains, which were curated in London and discussed by Boné and Singer (1965), Cooke and Coryndon (1970), Aguirre and Alberdi (1974), and Forsten (1996). Laetoli was further collected by Kohl-Larsen during his expedition to the Southern Serengeti in 1938–1939, and the material is housed in Berlin and described by Dietrich (1942).

Dietrich (1942) identified two taxa, *Hypsohipparion albertense* from the Vogel River and *Stylohipparion* sp. Dietrich (1941) erected the genus *Hypsohipparion* to describe a horse of relatively large size with rather hypsodont lower cheek teeth that lacked ectostylids. Arambourg (1947) questioned the validity of Dietrich's *Hypsohipparion* and suggested that the lower teeth attributed to this taxon (those lacking ectostylids) were derived from *Equus*. While Kohl-Larsen's collection are generally considered to contain material from unknown or mixed stratigraphic levels, Boné and Singer (1965) pointed out that most of the upper cheek teeth are hipparion and that the degree of contamination may be less than previously supposed.

The identification of *Stylohipparion* from Laetoli was based upon the presence of small-sized cheek teeth bearing ectostylids. Dietrich (1942) further observed that *Stylohipparion* was conspecific with *Eurygnathohippus*, the highly derived hipparion of Pleistocene age from Cornelia, South Africa (Van Hoepen 1930; Eisenmann 1983). Presumably this finding was based on a comparison between a mandibular symphysis from Laetoli and the symphysis from Cornelia, rather than the Olduvai specimens, as these were not discovered until the 1950s (OLD 55, BK II, 293, 067/5344). There is an equid symphysis with a low and flattened morphology from Gadjingero (Gadj. 10) that Forsten (1996) and Boné and Singer (1965) describe as lacking the third incisor and canine. All material from these early collections is of unknown stratigraphic provenance. However, this latter specimen may be derived from the Upper Ndolanya Beds, since Gadjingero is the equivalent of the present-day Locality 18, but it cannot be discounted that the specimen was derived from Pleistocene deposits that also occur in the Gadjingero River (see Harrison and Kweka 2011).

Eisenmann (1976, fig. 1) shows a bivariate plot of the proportions of the mandibular symphyses of a range of hipparion taxa including the Gadjingero specimen from Laetoli, which plots closely with a symphysis of *E. cornelianus* from Olduvai (067/5344). This suggests that the Gadjingero symphysis may be derived from *E. cornelianus*, except for the seemingly absent third incisors; perhaps these were originally present, but the alveoli are obscured by matrix. Cooke and Coryndon (1970) contended that only one taxon was represented at Laetoli and referred all material to *Hipparion albertense*, which is usually considered to be a *nomen vanum* on the basis of the inadequate type material (Hooijer 1975).

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Initially it was thought that the Laetoli deposits could be roughly correlated with Bed I and II at Olduvai until the discovery of hominin remains in 1974 (Leakey 1987). Detailed study of the local geology of the Laetoli area (Hay 1987; Leakey 1987) established a stratigraphic framework, which demonstrated that the "older fauna" was much earlier than previously supposed.

Further investigations in the Omo, Turkana, Olduvai and Laetoli regions during the 1970s led to a better understanding of hipparion systematics in East Africa (Hooijer 1975, 1976, 1987a, b; Hooijer and Churcher 1985; Hooijer and Maglio 1974; Eisenmann 1983).

After 1974, systematic collections of fossils at Laetoli with secure stratigraphic information stimulated further studies of the fauna. Hooijer (1979, 1987a, b) described almost one hundred hipparion teeth collected by Mary Leakey between 1974 and 1976. The 1979 paper was reprinted in the 1987 Laetoli monograph (Leakey and Harris 1987). After Hooijer's original report was completed he received further specimens from Mary Leakey, and these were published in the Laetoli volume. In this text we refer to Hooijer's original report as 1987a, and his additional analysis as 1987b.

Hooijer (1987a) identified two hipparion taxa from the Upper Laetolil and Upper Ndolanya Beds, although he refrained from giving a specific identity to the hipparion from the Upper Laetolil Beds, describing it as "*Hipparion* sp." Hooijer characterized this taxon as representative of the "Mpesida-Aterir" type hipparion, which he loosely correlated with the 7–4 Ma interval. This group included *Hipparion turkanense* from Lothagam, and a single specimen of this taxon from the Mursi Formation, Ethiopia, and material that Hooijer assigned to *H. primigenium* from Kanapoi and Ekora, which outcrop a few miles north and south of the Lothagam locality (Hooijer and Maglio 1974; Hooijer 1975).

The cheek teeth of the earlier group are generally larger, but not so hypsodont as later hipparions and have less well developed ectostylids on the permanent mandibular cheek teeth, when present. Hooijer found several features that characterized the upper cheek teeth such as bifid pli caballin, which is sometimes in contact with the protocone, but no single character to give this taxon a specific identity. These characters are generally primitive for Old World and, in particular, African hipparions.

Crown height of upper M1 is between 60 and 70 mm. Skulls from Kanapoi and Ekora have a preorbital fossa, whilst this is absent in the Lothagam skull of *Eurygnathohippus turkanense*, (KNM LT-136; figs. 9–7, Bernor and Harris 2003), and tends to be absent in later hipparions from East Africa. One small-bodied taxon was also reported from Lothagam, originally attributed to *H.* aff. *sitifense* by Hooijer and Maglio (1974) because its small size compared closely with the North African taxon from Saint Arnaud Cemetery, Algeria. Bernor and Harris (2003) cited Eisenmann's (V. Eisenmann, personal communication) observations that the St. Arnaud horse never had a type specimen designated and the assemblage has since been lost. Furthermore, the North African late Miocene has a number of small hipparions, and of these none compare in morphological details to the Lothagam small hipparion. As a result, Bernor and Harris (2003) assigned the Lothagam small hipparion material to *Eurygnathohippus feibeli.*

Ectostylids were not recorded from most of the permanent lower cheek teeth examined by Hooijer from the Laetolil Beds, but an associated tooth row (LAET 75-491) from Loc. 11 has ectostylids and is morphologically similar to dentitions of the same age (Hooijer 1987a). Ectostylids were found on an associated right lower dp3 and dp4 from Loc. 9S, Upper Laetolil (Hooijer 1987a), and deciduous premolars from the Upper Ndolanya Beds. Ectostylids are invariably present on hipparion deciduous teeth and accordingly have little phylogenetic significance in themselves (Hooijer 1975).

Hooijer (1987a) referred the material from the Upper Ndolanya Beds to *H.* cf. *ethiopicum*, after a taxon first described by Joleaud (1933) as *Libyhipparion ethiopicum* from unknown level(s) in the Omo. In Hooijer's (1975) revision of the "advanced hipparion" (*Stylohipparion*) group from eastern Africa he selected a single specimen from Joleaud's original type series as the lecotype for *H. ethiopicum*. This was a right m3 (Joleaud 1933, Plate 1, figs. 2 and 6, subsequently accessioned in the Museum National d' Histoire Naturelle, Paris [MNHN] as 1951-4-127), lacking specific stratigraphic provenance. The original material includes four additional topotypic lower cheek teeth. Three of these teeth seem likely to have been derived from the same individual as the lectotype. These cheek teeth may be characterized by their well developed ectostylids, angular, pointed metaconid-metastylids, as well as by their hypsodonty (Hooijer 1975). The metastylids of the associated cheek teeth are especially triangular in the Omo material and the ectostylids are more obliquely orientated than most material referred to this taxon. Protostylids and pli caballinid are also present. In many specific morphological characteristics, this material is similar to that from the Upper Ndolanya Beds, but otherwise they are similar to other mid-Pliocene and early Pleistocene African hipparion assemblages. The lack of complete metapodials, premaxillae with incisors and mandibular symphyses with incisors disallows any specific referral to other relevant hipparion assemblages. In effect, neither the temporal context nor the morphological features are sufficient to compare or verify the taxonomic identity of *Eurygnathohippus* "*ethiopicus*".

Hooijer considered the mandibular and maxillary symphyses recovered from site BK, Bed II, Olduvai, as the same taxon as the mandibular symphysis from Cornelia, South Africa described by van Hoepen (1930) as *E. cornelianus*. The further discovery of a skull from the BK locality in 1973 (2845/2846) convinced Hooijer that *Stylohipparion* and *Eurynathohippus* were congeneric. However, Hooijer retained the nomen *ethiopicum* (Hooijer 1975; Hooijer and Churcher 1985) because he acknowledged that differences between the northern, southern and eastern forms might exist, but that they could only be differentiated when further skulls were found. Hooijer concluded that if a different generic name was required it should be *Eurygnathohippus.* We agree.

Despite Hooijer's best efforts, the taxonomy of the African hipparions is still incompletely resolved. The earlier hipparion group dating from the 7–4 Ma have generally larger cheek teeth and lack ectostylids, or if these are present they are small. Later hipparions are characterized by having smaller sized lower teeth with well developed ectostylids. These characteristics are thought to indicate the "advanced stage of evolution" as seen in *Stylohipparion* (Hooijer 1975). The genus *Stylohipparion* was first erected by van Hoepen (1930) for material from Cornelia, South Africa but it has also been used to describe a grade of evolution that categorizes African Pleistocene hipparions.

The occurrence and size of ectostylids upon the lower cheek teeth of Plio-Pleistocene hipparions has been considered an important source of taxonomic and paleoecological information (Hooijer 1975). Small, inconstant ectostylids from lower cheek teeth have been reported from a series of Pliocene localities, including Kanapoi, Chemeron Formation, locality J.M. 493 (Hooijer 1975) and it has been shown how these become a constant feature and enlarge in size through the Plio-Pleistocene (Hooijer and Churcher 1985). Boné and Singer (1965) found that ectostylids are particularly constant in p4 and m1.

Presence or absence of ectostylids has been used to assign teeth at the specific level. However, this may be problematic. First, the frequency of ectostylids varies between populations. Early African hipparions have small (length and width) and short (height) ectostylids and unless the tooth is well worn, the ectostylid does not present on the occlusal surface. However, in early populations one can often discern an ectostylid "bulge" on the labial aspect of the crown. Ectostylids become longer and wider and ascend higher on the crown in the medial Pliocene, as exhibited in the 3.4–2.9 Ma assemblages at Hadar, Ethiopia. Beginning around Upper Ndolanya Beds time, 2.66 Ma, African hipparions have longer, wider and higher crowned ectostylids and it is at this time that they are persistent and usually visible features on the hipparion crown (Bernor and Armour-Chelu 1999; Bernor and White 2009).

Of further relevance is the taphonomy of equid cheek teeth. Equid cheek teeth are extremely resilient and become incorporated into fossil concentrations with many years of time represented. When teeth from time successive horizons become mingled frequency counts can only be seen as estimates subject to a wide margin of error. An example of this type of problem is shown at Laetoli where ectostylids were originally considered absent in the lower cheek teeth derived from the Laetolil Beds. Further collecting by Harrison has recovered a few specimens bearing ectostylids from the early part of the sequence, where they were formerly considered absent (Hooijer 1987a).

In the original description of the *Eurygnathohippus* type specimen van Hoepen (1930) mistook the third incisor for a canine tooth; this was subsequently corrected by Cooke (1950). Hooijer (1975) and others questioned whether the advanced representatives of *Eurygnathohippus* possessed canines, but they are now known to be present in two mandibles, likely male individuals, from Koobi Fora and Laetoli (Eisenmann 1976; Hooijer 1987a). The canines preserved in the Laetoli specimen (LAET 74-253, Loc. 18) show they were directly tucked behind the third lower incisor (Hooijer 1987a, Plate 9.1). Canine teeth are not yet recorded from maxillary dentitions, including the 2845/2846 skull from BK, Bed II Olduvai, and it is possible that canines are absent in later representatives of the species.

This present study includes material collected by Terry Harrison between 1998 and 2005 and some specimens collected by Mary Leakey and curated in the National Museum of Tanzania in Dar es Salaam. The oldest material, from the Lower Laetolil Beds, derives from localities at Esere, Noiti 3 and Kakesio, dating to around 3.85–4.4 Ma. Material from the Upper Laetolil Beds dates from 3.6 to 3.85 Ma and the younger material from the Upper Ndolanya Beds (at Locs. 7E, 14, 15, 18, 22S, 22E) is dated at 2.66 Ma (Deino 2011) and mixed deposits occur at Locs. 15 and 22E.

Abbreviations, Definitions and Methods

AMNH	American Museum of Natural History, New York
KNM	Kenya National Museum, Nairobi
MA	Middle Awash Project, Ethiopia
MNHN	Museum National d'Histoire Naturelle, Paris
SAM	South African Museum of Natural History, Cape Town
SMNK	Staatliches Museum für Naturkunde, Karlsrhue

The taxon hipparion has been applied in a variety of ways by different authors. We utilize the following definitions in this work: 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* (= senior synonym of "*Stylohipparion*"), *Proboscidipparion*, "Plesiohipparion." Characterizations of these taxa can be found in MacFadden (1984), Bernor and Hussain (1985), Webb and Hulbert (1986), Hulbert (1988), Hulbert and MacFadden (1991), Qui et al. (1988), Bernor et al. (1988, 1989, 1996, 1997, 2003, 2005, 2008, 2010), Bernor and Armour-Chelu (1999), Bernor and Harris (2003), Scott et al. (2005a, b), Armour-Chelu et al. (2006), Bernor and Kaiser

(2006), Kaiser and Bernor (2006), Woodburne (1989, 2007), Woodburne (2007) and previous publications by him cited therein.

Hipparion s.s.: The name is restricted to a specific lineage of horses with the facial fossa positioned high on the face (MacFadden 1980, 1984; Woodburne and Bernor 1980; Woodburne et al. 1981; MacFadden and Woodburne 1982; Bernor and Hussain 1985; Bernor 1985; Bernor et al. 1987, 1989, Bernor et al. 2008, 2010; Woodburne 1989). The posterior pocket becomes reduced and eventually lost, and confluent with the adjacent facial surface (includes Group 3 of Woodburne and Bernor 1980). Bernor's definition departs from some investigators in not recognizing North American species of *Hipparion* s.s. Bernor (1985) and Bernor (in Bernor et al. 1989) have argued that any morphologic similarity between North American "Hipparion s.s." and *Hipparion* s.s. is due to homoplasy.

"Hipparion": several distinct and separate lineages of Old World hipparionine horses once considered to be referable to the genus *Hipparion* (Woodburne and Bernor 1980; MacFadden and Woodburne 1982; Bernor and Hussain 1985; Bernor 1985; Bernor et al. 1980, 1988, 1989).

"Cormohipparion" as explicitly used herein: not determinable as strictly a member of the *Cormohipparion* lineage as recently defined by Woodburne (2007). As such, we recognize the likely paraphyly of North and East African "Cormohipparion" *africanum* and the possibility that it will be assigned to a new genus as the result of a detailed phylogenetic analysis. However, "Cormohipparion" *africanum* is determined to exhibit a morphologic pattern closest to *Cormohipparion* and not the *Hipparion* s.s., *Hippotherium*, *Eurygnathohippus* clades, or any other Old World clade recognized by us or previous authors. Phylogenetic systematic studies are underway that will likely allow eventual assignment of African "Cormohipparion" to a known, or new genus rank (Wolf and Bernor, in progress).

Hipparion: purposely not capitalized and used as a non-formal taxonomic abbreviation for hipparionine.

Measurements are in mm. All postcranial measurements are as defined by Eisenmann et al. (1988) and Bernor et al. (1997) and rounded to 0.1 mm; all dental measurements are as defined by Bernor et al. (1997). The osteological nomenclature, 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. Hipparion monographs by Gromova (1952) and Gabunia (1959) were consulted after the French translations. Log10 ratio diagrams were calculated and plotted in Excel 2008 for MAC (MacIntosh OSX).

Abbreviations in Text

Ma: mega-annum in the geochronologic time scale

Africa: ages in m.y. usually based on radio isotopic analyses or magnetostratigraphic analyses. North Africa: localities may be referred to the MN biochronologic time scale.

North America: Hemingfordian, Barstovian, Clarendonian, Hemphillian, Blancan; intervals of the North American land mammal age sequence (e.g., Woodburne 1987, 2004), based on characteristic associations of mammalian taxa. Western Eurasia: Vallesian, Turolian, and Ruscinian; intervals of the European land mammal age sequence, commonly termed units (*sensu* Fahlbusch 1991).

Measurement Table Abbreviations

Sex: M = male; F = female; ? = unknown. Sex can be defined by the size of a canine tooth, male being large, female being small.

Side: lt. = left; rt. = right

Element abbreviations: MCIII = metacarpal III; premax = premaxilla; MTIII = metatarsal III; MPIII = Metacarpal III or metatarsal III; 1PHIII = First phalanx III (central digit) of either the anterior or posterior limb, which are difficult to distinguish in hipparion.

tx = maxillary tooth; tm = mandibular tooth; mand = mandible. M1-M38 refers to measurements as described by Eisenmann et al. (1988) and Bernor et al. (1997).

Many figures present plots with abbreviations for different taxa and fossil samples. These abbreviations are as follows:

General Analyses

A = Awash (Middle), Ethiopia
B = Baringo Basin, Kenya
C = Langebaanweg, South Africa
D = Abu Dhabi
E = Eppelsheim, Germany
G = Omo, Ethiopia
H = Hoewenegg, Germany
I = Laetoli, Tanzania
K = Ekora, Kenya
L = Lothagam, Kenya
O = Olduvai, Tanzania
M = Manonga Valley, Tanzania
P = Potwar Plateau, Pakistan

R = Hadar, Ethiopia
S = Sahabi, Libya
T = Sinap, Turkey
U = Uganda
Z = Morocco

Abbreviations for Laetoli Horizons

N = Upper Ndolanya Beds
U = Upper Laetoli Beds
L = Lower Laetoli Beds
P = No provenance

Metric Procedures

Measurements are all given in millimeters and rounded to 0.1 mm. Measurement numbers (M1, M2, M3, etc.) refer to those published by Eisenmann et al. (1988) and Bernor et al. (1997) for the skulls and postcrania. Tooth measurement numbers refer to those published by Bernor et al. (1997) and Bernor and Harris (2003).

Bernor and Armour-Chelu (1999), Bernor and Harris (2003), Bernor and Scott (2003), Bernor et al. (2004, 2005, 2010) Gilbert and Bernor (2008), Bernor and Haile Selassie (2009) and Bernor and White (2009) have compared African hipparions to an extensive series of Late Miocene-Pleistocene Eurasian and African assemblages. In various studies, Eisenmann, (see Eisenmann 1995 for a comprehensive summary), has used log 10 ratio diagrams to evaluate differences in hipparion metapodial proportions as a basis for recognizing taxa and their evolutionary relationships. Bernor et al. (2003) and Bernor and Harris (2003) have used multiple statistical tests, including univariate, bivariate and multivariate statistics as well as log 10 ratio diagrams to evaluate and resolve the alpha systematics of hipparionine horses. Bernor et al. (2005) used log 10 ratio diagrams together with multivariate statistics to evaluate metapodial and first phalangeal evidence for postcranial evolution in Ethiopian hipparions. We incorporate these previously used methodologies in this work.

Our statistical analysis uses two recognized population standards. For postcrania we use the skeletal population from Höwenegg (Hegau, southern Germany, 10.3 Ma; Bernor et al. 1997) for calculating 95% confidence ellipses used in bivariate plots, and log10 mean standard values for all log10 ratio diagrams (MPIIIs and 1PHIIIs). We use the Eppelsheim standard for calculating 95% confidence ellipses for cheek tooth variables (Bernor and Franzen 1997; Kaiser et al. 2003; Bernor and Harris 2003).

Statistical Analysis

Tables 12.1–12.3 provide measurements of the Laetoli specimens used in this analysis. Comparative measurements were taken from Bernor's unpublished equid database. Analyses of Laetoli Equidae included bivariate plots of maxillary P2, calcanea, astragali, MC III, MT III and 1PHIII. All of these skeletal elements are clearly differentiated with the exception of 1PHIII. While anterior and posterior 1PHIII can be clearly differentiated in living *Equus*, the same cannot be said for all hipparions. The Höwenegg hipparion skeletons were found in articulation and thus the anterior versus a posterior 1PHIII are known. However, the statistical differences between these phalanges are minor at best, which has led us to analyze all 1PHIII together. Some advanced African hipparions may in fact differ significantly in anterior versus posterior 1PHIII dimensions, but this has not been adequately demonstrated. Bivariate plots will include two parallel sets of plots: one of our broad Eurasian – African samples to provide relevant ranges of variability in the sample under consideration, and the other that is specifically targeted to variability in the Laetoli sample by stratigraphic unit. The statistical analysis will be followed by the description of the material by stratigraphic horizon.

Metrical Results

Maxillary P2

Bernor et al. (2003) argued that P2 is the best tooth to statistically analyze for length and width measurements because it varies the least in these dimensions throughout ontogeny. Figure 12.1a is a bivariate plot of maxillary P2 occlusal width (measurement M3) versus occlusal length (measurement M1) for a large sample of African hipparions. Most of the sample falls within the Eppelsheim 95% confidence ellipse, with the largest specimens falling outside and above the ellipse originating from the Middle Awash, Potwar Plateau and Hadar. The smallest specimens, found just outside the lower border of the ellipse are from Lothagam and the Middle Awash. Figure 12.1b compares the known P2s from the Upper Ndolanya Beds and Upper Laetolil Beds; all specimens fall either within or just inside the Eppelsheim ellipse and are neither extraordinarily large, nor small. Cheek teeth are highly variable and change in size and shape becoming progressively smaller and square in outline with age. This is particularly the case with the advanced, high crowned hipparions that occur during the late Pliocene and Pleistocene of Africa (Bernor et al. 2010).

Table 12.1 Measurements (mm) of *Eurygnathohippus* aff. *hasumense* specimens from the Laetolil Beds, Laetoli (Tooth measurements after Bernor et al. 1997; Bernor and Harris 2003 – see text for further description of measurements). Loc=Laetoli collecting locality. KK=Kakesio; ES=Esere; N3=Noiti 3

Specimen	Loc	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
Upper deciduous fourth premolar															
EP 1405/03	8	28.7	28.1	17.7		26.7									
EP 1013/98	9S	30.7	28.1	25.7	26.2	16.3	4.0	5.0	2.0	1.0	9.4	4.9			
LAET 75-2024	10	31.1		20.9		27.7									
EP 2321/03	13	33.8	31.7	21.6	24.0	27.4		2.0	1.0		8.3	3.5			
Upper second premolar															
EP 2989/00	1	28.2	26.1	29.6	28.5	38.6	1.0	6.0	1.0	1.0	16.6	10.0			
EP 1367/00	6	34.0	33.2	22.9	0.0	13.0	2.0	1.0	3.0	0.0	13.1	8.3	4.4		
EP 1967/00	6	24.1	21.8	25.5	26.4	15.9	0.0	5.0	2.0	0.0	10.8	5.4			
LAET 75-3534	8	38.7	37.8	25.9	26.6	24.7	2.0	2.0	0.0	0.0	9.1	5.6			
EP 512/98	10	35.5	32.7	25.9	21.3	54.2	3.0	3.0	0.0	0.0	9.7	4.1			
EP 404/00	12	37.6	36.8	0.0	23.8	35.6	2.0	2.0	2.0	1.0	11.6	0.0			
EP 071/98	KK	65.6	27.9	8.8	22.1										
Upper third/Fourth premolar															
LAET 78-5231	8	34.3	26.7	8.84	25.3										
EP 3531/00	12E	29.3	27.5	28.4	29.0	40.4	1.0	5.0	3.0	1.0	11.3	5.6			
EP 3532/00	12E	29.1	28.2	28.0	28.4	42.6	3.0	5.0	3.0	1.0	11.5	4.9			
Upper third premolar															
EP 2989/00	1	28.2	26.1	29.6	28.5	38.6	1.0	6.0	1.0	1.0	16.6	10.0			
EP 1706/04	2	31.5	25.9	30.0	27.2	52.8	3.0	7.0	4.0	1.0	8.5	3.4			
LAET 75-2114	2	27.8	26.0	25.6	23.6	26.5					9.4	4.5			
EP 1967/00	5	24.1	21.8	25.5	26.4	15.9	0.0	5.0	2.0	0.0	10.8	5.4			
EP 1969/00	5	26.3	23.1	24.7		41.2					10.2	4.7			
LAET 75-1193	6	28.4	26.7	23.3	51.7						9.8	3.8			
EP 1186/98	9	26.5	26.7	27.6	22.7	0.0	2.0	1.0	0.0		10.7	5.3			
EP 1187/98	9	24.7	24.6	24.9	26.3	28.9	1.0	5.0	0.0	0.0	10.0	4.4			
LAET 75-1430	9S	29.2	23.5	26.2	25.1	58.1	4.0	4.0	1.0	1.0	11.8	3.9			
LAET 75-3583	9S	29.9	26.5	27.0	24.8	49.8					8.4	3.1			
EP 1431/01	12	29.8	28.4	29.6	26.7	36.5	1.0	5.0	5.0	1.0	10.2	4.7			
EP 3531/00	12E	29.3	27.5	28.4	29.0	40.4	1.0	5.0	3.0	1.0	11.3	5.6			
EP 3532/00	12E	29.1	28.2	28.0	28.4	42.6	3.0	5.0	3.0	1.0	11.5	4.9			
EP 1443/01	21	29.2	29.0	23.1	21.2	38.4	3.0	4.0	1.0		9.6	4.3			
LAET 75-3437	21	27.3	24.9	24.1		39.4					9.4	4.7			
Upper fourth premolar															
EP 435/04	2	28.2	24.0	26.9	27.8	65.1	5.0	5.0	3.0	2.0	65.1	9.7			
EP 4222/00	2	29.7	25.4	23.8	25.8	66.9	2.0	5.0	1.0	0.0	8.9	3.4			
EP 1967/00	5	23.0	22.0	23.7	25.4	14.9	0.0	4.0	3.0	0.0	9.5	4.4			
EP 1420/04	6	27.3	25.9	31.5	22.7	0.0	6.0	0.0	0.0		9.8	5.6			
EP 1494/98	9	29.0	25.6	25.2	29.1	60.5	1.0	4.0	3.0	1.0	10.9	3.1			
EP 1012/98	9S	26.1	23.7	21.1	20.9	43.4	2.0	6.0	2.0	2.0	8.3	3.8			
EP 978/03	10	24.1	22.3	24.1	24.5	43.1		5.0	1.0	2.0	9.7	4.3			
LAET 75-2070	10	27.7	24.5	22.9	64.2	1.0	3.0	1.0	1.0		9.8	3.7			
EP 205/98	10E	24.7	23.3	26.1	25.8	49.7	3.0	6.0	3.0	1.0	8.5	4.3			
EP 1606/00	10W	27.1	24.3	29.2	28.3	32.5					9.9				
EP 1553/98	10E	26.3	24.6	28.1	28.0	25.9	1.0	10.0	2.0	1.0	9.4	5.1			
EP 420/01	13	25.4	24.4	24.0	25.5	28.0	3.0	5.0	2.0	1.0	9.2	4.2			
LAET 75-3358	21	28.1	22.6	25.2	25.4	65.8					8.0	3.9			
LAET 75-3667	22	23.7	23.3	24.3	24.1	20.3	1.0	4.0	1.0		9.9	5.0			

(continued)

Table 12.1 (continued)

Specimen	Loc	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
Upper first molar															
EP 435/04	2	26.2	22.8	24.5	25.9	62.6	4.0	5.0	4.0	1.0	62.4	9.2	3.9		
EP 685/00	2	27.9	23.9	23.1	23.2	68.1	1.0	3.0	3.0	0.0	10.2	3.0			
EP 959/05	2	28.1	25.1	23.7	24.0	68.0	1.0	5.0	1.0	1.0	9.4	4.4			
EP 1967/00	5	22.6	22.3	22.6	23.8	18.3	0.0	4.0	3.0	1.0	9.5	4.6			
EP 1942/03	7	24.0	22.1	23.4	25.1	24.5	1.0	4.0	2.0	0.0	9.6	4.9			
LAET 75-1320	8	25.8	23.4	25.1	25.0	52.6									
EP 766/03	9	26.8	24.4			68.5	4.0	6.0	1.0	3.0					
EP 2422/03	9S	23.6	23.9	21.7	23.9	32.7	1.0	4.0	1.0		10.0	4.6			
EP 172/99	10	23.5	22.9	23.8	24.7	30.9	0.0	3.0	2.0	1.0	9.0	5.0			
EP 1326/98	13	31.2	28.1	25.3	29.2	75.4	1.0	6.0	4.0	1.0	11.6	3.9			
LAET 75-3187	20	27.3	22.9	23.5	26.5	68.2		5.0	3.0	2.0	9.3	3.9			
EP 198/03	KK	27.8	22.8	23.5	23.9	63.1					9.4	3.6			
Upper second molar															
EP 4222/00	2	63.4	30.1	11.1	25.2										
EP 1967/00	5	20.5	23.5	10.5	25.1										
EP 1694/00	5	25.2	23.8	23.3	23.4	58.2	2.0	4.0	3.0	0.0	8.3	3.9			
LAET 75-1052	7E			21.1	20.8	63.4	2.0	4.0	1.0	3.0	10.3	3.1			
LAET 75-3532	8	25.4	22.2	23.3	24.1	60.9	3.0	5.0	3.0	2.0	10.4	3.6			
EP 764/03	9	25.5	25.3	22.7	22.8	45.5	5.0				9.1	4.0			
EP 765/03	9	26.3	24.9	21.3	24.0	72.7	2.0	2.0	2.0	1.0	10.0	3.6			
EP 1011/98	9S	24.9	22.2	22.0	24.1	35.2	1.0	4.0	1.0	0.0	8.8	4.1			
LAET 75-1450	9S	28.0		23.3		76.3									
LAET 75-1529	9S	25.7	22.7	24.0	25.1	59.8	3.0	5.0	3.0	1.0	9.8	4.0			
EP 171/99	10	24.5		23.8			2.0	10.0	3.0	1.0					
EP 513/98	10	23.0	22.1	21.4	23.4	22.9	0.0	5.0	0.0	0.0	9.2	4.2			
LAET 75-1781	10W	24.9	21.5	22.5	23.1	65.5	1.0	6.0	1.0	1.0	10.6	3.4			
EP 071/98	KK	26.8	23.5	22.2	25.3	59.4			2.0	1.0	8.2	4.4			
EP 086/98	KK	25.8	24.7	22.2	25.6	41.2	4.0	7.0	3.0	1.0	8.7	4.0			
Upper third molar															
EP 81/04	2	23.7	25.4	15.7	20.7	67.4	0.0	0.0	0.0	0.0	8.7	2.6			
EP 434/04	2	25.4	26.5	21.4	22.8	54.5	4.0	7.0	3.0	1.0	8.6	3.6			
EP 502/01	2	23.0	27.9	20.1	23.2	60.1	3.0	2.0	2.0	2.0	9.1	3.4			
EP 1842/00	2	26.0	25.5	21.5	22.5	35.8	2.0	5.0	3.0	1.0	11.2	4.2			
LAET 78-5068	2	23.4	25.3	17.6	20.8	63.3	2.0	4.0	1.0	0.0	11.1	2.3			
EP 1606/00	3	25.7	26.8	21.9	21.7	53.4					8.6	3.6			
EP 1967/00	5	26.4	26.7	20.8	20.8	23.3					10.9	4.1			
EP 1419/04	6	23.5	22.6	18.5	20.9	28.2	1.0	6.0	1.0	1.0	9.3	3.9			
EP 1185/98	9	27.2	24.6	21.2	23.0	19.2	1.0	5.0	3.0	1.0	12.4	3.9			
LAET 75-1991	10E	23.3	23.3	19.3	20.9	48.6	3.0	3.0	4.0	1.0	8.6	3.6			
EP 625/04	10W	25.6	27.1	20.3	24.0	44.0		5.0	3.0	1.0	9.7	3.8			
EP 698/05	10W	24.6	23.0	20.0	19.5	18.9	0.0	4.0	0.0	0.0	10.5	4.7			
EP 1295/03	11	24.0	25.2	20.4	21.3	41.7	3.0	5.0	3.0	1.0	9.4	2.3			
EP 533/05	12	22.9	25.7	20.1	19.5	53.2		2.0	1.0		7.4	3.2			
EP 403/00	12E	26.5	29.3	22.0	23.9	49.8	3.0	3.0	3.0	1.0	12.6	3.6			
EP 1512/03	12E	26.4	28.0	21.1	23.8	52.4									
EP 2043/00	13	25.6	25.8	21.8	22.7	41.2	1.0	6.0	2.0	1.0	8.5	3.4			
EP 2361/03	13E	28.9	29.3	22.3	24.8	38.3									
EP 161/04	15	24.1	26.1	20.9	21.8	36.7	4.0	5.0	1.0	1.0	8.1	3.8			

(continued)

Table 12.1 (continued)

Specimen	Loc	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
Lower second deciduous premolar															
EP 977/04	16	37.3	36.3	15.0	11.6	15.6	14.5	16.4	11.4	13.4	9.2	6.0	2.2	6.9	
Lower fourth deciduous premolar															
EP 977/04	9	30.9		13.4	9.1	11.0	16.3	16.9	12.5	12.0	11.8	9.0	3.4	7.6	
Lower second premolar															
EP 1190/98	9			13.1	9.7	10.2	14.4	15.1	12.4	13.0	31.6	5.9	2.0	37.3	
EP 1192/98	9	29.7	29.8	13.4	6.7	14.4	14.3	14.4	12.1	13.8	24.3				
LAET 75-1431	9S	32.1	31.3	15.6	10.3	16.5	15.8	13.5	12.3	14.4	31.8				
EP 1015/98	9S	29.4	28.3	14.2	8.4	16.3	15.3	15.0	12.6	13.5	42.2				
Lower fourth premolar															
LAET 81-48	9S	27.6	25.7	16.2	8.8	14.9	17.0	15.1	14.7	15.3	49.6				
EP 1016/98	9S	29.4	27.7	18.1	9.1	16.6	15.2	15.3	15.9	43.9					
EP 321/05	10W	26.8	26.8	24.8	16.1	9.1	11.5	16.8	17.5	15.1	14.2	29.3			
EP 617/98	10W	26.4		15.9	9.1	13.1	17.1	16.1	14.2	14.4					
EP 790/98	10W	24.5	24.0	15.4	8.3	9.6	15.7	15.8	13.5	12.8	18.5				
EP 3170/00	10W	25.1	24.3	14.5	8.4	11.0	14.1	12.6	12.7	12.0	26.3				
EP 594/00	22E	27.7	27.1	16.5	8.1	17.1	16.7	15.9		14.9	51.3				
Lower first molar															
LAET 76-3983	2	24.7	22.6	14.7	6.3	9.1	14.6	16.8	13.9	13.4	15.1				
LAET 78-5008	2	28.0	26.7	17.7	9.3	11.9	13.8	14.8		12.9	55.4				
LAET 76-4041	5	26.8		16.0	8.5	11.1	11.0		12.4	12.3					
EP 1496/98	9	24.7	24.5	14.8	8.8	10.7	13.0	13.9	12.0	11.6	47.1	3.8		45.4	
EP 1216/04	9S	25.4	23.4	16.5	7.8	11.4		15.2	15.3	13.6	35.9				
EP 2452/00	13E	27.2	23.4	15.2	8.1	10.8	13.1	14.5	12.6	11.9	35.9				
EP 3606/00	21	26.9	22.9	15.0	6.7	9.8	14.0	15.5	10.7	13.5	42.7				
EP 3732/00	22	27.7	24.4	12.9	7.5	10.3	11.6	12.0	10.0	8.6	65.1				
Lower second molar															
LAET 78-4974	2	25.4	25.3	15.1	7.4	12.2	15.3	15.6	16.1	15.0	26.8				
EP 2196/03	7	26.1	25.0	15.0	8.5	9.2	14.8	15.3	13.4	12.2	28.1				
EP 1017/98	9S	28.2	27.0	14.8	8.6		18.3	13.6	15.1	15.9	63.2				
EP 2480/00	13	26.1	25.1	15.7	8.1	9.1	12.8	13.5	12.7	12.6	42.1	3.0	1.7	37.5	
Lower third molar															
EP 2196/03	7	30.2	30.4	14.4	7.7	10.2	12.6	12.7	12.9	10.4	25.7				
EP 1241/01	9S	27.3		13.2	8.1	10.3	12.6	13.0	12.7	11.5	40.3				
EP 1242/01	9S	25.6	27.6	12.8	6.7	9.3	10.9	12.1	10.6	9.6	68.6				
LAET 75-3667	22	28.0	22.7	21.4	20.1	17.7	1.0	2.0	1.0	1.0	11.4	5.3			
Metacarpal III															
EP 1528/00	3										38.8	39.2	32.1	28.4	30.0
LAET 75-1128	6					47.3	34.4	41.4							
EP 1107/00	8					44.5	32.1	41.0	11.9	7.0					
EP 4123/00	8														
EP 1244/01	9S										45.0	43.8	29.9	25.3	27.0
LAET 75-2250	10E					47.5	31.5								
LAET 78-4752	11										46.2	43.6	35.0	28.5	29.6

(continued)

Table 12.1 (continued)

Specimen	Loc	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
Metacarpal III															
LAET 75-1589b	13			30.6	27.9	46.7	34	40.2	11.3	5.4					
LAET 75-3138	12					45.5	33.1	40.2	10.7	6.0					
LAET 75-1589	13					45.6	33.6	41.4	10.5	5.8					
LAET 75-3442	21					47.6	35.6	43.2	10.8						
EP 1222/98	22														
EP 1668/98	ES										42.4	38.7			
Tibia															
LAET 75-2891	4							72.9	51.6						
EP 300/00	8							73.0	52.2						
EP 146/98	10E							75.0	51.5						
Calcaneus															
LAET 75-2549	2			18.1			60.5	54.3							
LAET 75-1886	10			22.9			57.5	48.1							
EP 2572/00	11			23.2			49.3								
EP 2454/00	13E	115.9	76.1	22.3	28.4	50.9	58.4	44.8							
EP 1748/03	22			22.6			55.6	55.5							
Astragalus															
EP 678/00	2	62.1	62.5		62.9	49.5	38.9	52.0							
LAET 75-1897	2	66.8	63.7	31.4	66.8	55.6	38.8	56.4							
LAET 75-2530	2	65.2	66.8	30.8	64.1	54.0	37.4								
LAET 75-3756	6	62.9	63.7	34.6	62.2	51.2	36.2	46.9							
EP 3822/00	6	63.1	63.9	32.8	63.9	49.2	36.8	53.2							
EP 307/00	8	64.4	62.1	30.6	61.8	49.1	37.4	49.0							
LAET 75-1244	8	62.7	61.7	30.9	62.2	49.0	35.7	50.0							
LAET 75-1498	9	62.1	60.0	29.1	61.7	47.1	35.4								
EP 655/98	10W	61.3	57.1	30.1	48.8	48.5	34.3								
EP 3171/00	10W	59.9	59.8	28.3	56.2	46.2	35.2	46.2							
EP 364/98	10E	69.0	69.7	33.8	65.2	51.2	38.8	49.0							
LAET 75-3145	12	69.9	68.1	34.0	70.1	53	38.6	53.9							
EP 1130/04	13	61.3	62.1	31.9	61.4	47.9	35.2								
LAET 75-2944	16	66.1	67.3	31.5	58.5	55.8	38.3								
EP 1422/01	21	61.9	57.2	30.8	64.8	44.3	34.2	44.0							
LAET 75-3670	22	63.5	61.6	30.1	61.4	55.2	36.4								
Metatarsal III															
EP 2197/03	7										47.8	44.2	32.9	31.4	32.1
EP 3881/00	7														
EP 4122/00	8										43.2	41.0	34.5	26.9	31.5
EP 128/98	10E					45.02									
EP 558/00	22												33.6		29.8
EP 1669/98	ES										44.0	44.1	35.9	29.6	31
EP 463/04	N3					45.5	37.4	42.3	10.1	7.2					
First phalanx (1 ph3)															
EP 4221/00	2				46.5	32.9				26.4					
LAET 78-5160	9	68.6	61.2		48.0	33.6	40.0	39.6	24.0	22.7					
EP 893/00	10W	67.5	59.9	29.6			38.5	36.9	23.4	20.5	46.3	46.4	11.9	11.9	
EP 2481/00	13	70.7	63.0	33.0	47.6	37.6	40.1	40.5	24.5	15.2	41.4	47.3	17.4	16.5	

Table 12.2 Measurements (mm) of *Eurygnathohippus* aff. *cornelianus* specimens from the Upper Ndolanya Beds, Laetoli (Tooth measurements after Bernor et al. 1997; Bernor and Harris 2003 – see text for further description of measurements). Loc = Laetoli collecting locality. SA = Silal Artum

Specimen	Loc	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
Upper fourth deciduous premolar															
EP 445/05	18	31.5	28.9	13.9	9.9	10.6	13.8	14.5	8.9	8.6	23.6			19.3	
Upper first incisor															
LAET 75-2461	14	23		11.5		29.5									
EP 032/03	SA	17.3	11.1	14.7	14.6	29.6									
Upper second incisor															
LAET 78-5117	7E	12.3	13.8	13.5	13.7	24.5									
Upper third incisor															
LAET 75-3793	7E	31.2	17.9	10.9	11.6	33.8									
EP 1495/04	22E	18.3	11.3	13.1	12.3	34.6									
Upper second premolar															
LAET 75-2458	14			25.1		53.5					11.0				
EP 1033/00	15	35.4		22.5		60.0									
LAET 78-4872	18	32.1	29.9	23.8	21.3	30.4	2.0	1.0	2.0	1.0	7.7	4.8			
EP 781/01	18		32.4	22.7	22.9	29.4					6.8	3.9			
Upper third premolar															
EP 1213/03	7E	23.1	23.3	25.3	23.5	22.1	1.0	6.0	6.0	1.0	8.1	3.5			
EP 4010/00	7E	20.0	18.5	20.6	21.6	30.1	1.0	5.0	1.0	1.0	9.1				
EP 4011/00	7E	22.7	21.3	25.2	26.1	30.8	1.0	6.0	4.0	1.0	9.5	5.4			
EP 1183/04	14	26.5	23.0	24.9	27.3	43.0					7.2	2.9			
LAET 78-5049	14	28.9	25.5	28.3	25.3	69.7									
EP 1033/01	15	29.5				58.3									
EP 980/00	18	26.4	23.7	25.4	23.5	24.3	1.0	6.0	7.0	1.0	8.5	4.3			
EP 986/00	18	25.3	24.5	27.3		42.8					8.0	4.9			
LAET 78-4872	18	22.3	20.6	21.8	23.3	29.4	4.0	7.0	2.0	1.0	8.3	4.2			
EP 1495/05	22	24.8	21.5			19.1		4.0							
EP 1308/98	22S	24.1	23.0		23.6	40.9	3.0	3.0			7.3	3.7			
Upper fourth premolar															
LAET 75-906	7E	23.6	23.4	24.3	24.3	12.8	0.0	4.0	1.0	0.0	10.8	6.7			
EP 1213/03	7E	23.4	22.5	22.8	23.5	17.7	1.0	5.0	3.0	1.0	9.6	4.5			
LAET 75-1696	14	25.5	25.4	25.9	26.1	34.7	1.0	7.0	5.0	1.0	8.7	3.9			
EP 986/00	18	27.9	0.0	26.6	0.0	49.9	0.0				8.5	4.4			
Upper first molar															
EP 4018/00	7E	21.1	20.2	21.3	21.9	40.0		6.0	4.0	1.0	8.3	3.2			
EP 3470/00	15	29.0	22.6	22.9	23.7	80.0									
EP 986/00	18	25.6	24.1	25.2		51.2									
Upper second molar															
LAET 75-1685	14	25.4	19.7	23.1	73.4		4.0	2.0		10.9	3.6				
EP 1517/01	SA	23.6	22.1	22.0	23.4	50.2									
Upper third molar															
LAET 75-1639	14	25.5	27.4	20.1	22.6	50.3	1.0	2.0	1.0	1.0	9.1	3.5			
LAET 78-4872	18	21.8	22.3	18.9	18.8	33.5	3.0	4.0	4.0	1.0	7.9	3.3			
EP 1495/04	22E	23.6	23.2	19.7	19.9	28.3		4.0			10.0	4.0			

(continued)

Table 12.2 (continued)

Specimen	Loc	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
Lower first incisor															
LAET 78-4815	18	14.7	12.3												
Lower second premolar															
EP 4012/00	7E	31.2	31.7	13.7	6.3	13.9	16.2	17.8	11.7	13.8	24.4	5.5	3.6	19.6	
LAET 81-73	14	31.3	30.8	12.0	7.0	13.9	13.5	15.4	10.3	12.3	19.0	6.4	3.6	14.1	
LAET 75-3765	14			14.8		14.6	16.0	16.1		14.0	23.1	5.1	3.6	19.3	
LAET 78-4815	18	30.7	30.5	13.2	3.9	15.5	12.8	15.3	10.6	11.4	16.3	8.5	3.8	18.0	
Lower third premolar															
LAET 78-4815	18	25.2	23.0	15.6	8.6	13.0	15.4	15.2	14.3	12.1	13.8	8.0	3.0		
Lower fouth premolar															
LAET 78-4815	18	24.4		15.3	8.5	11.4	16.1		14.6	12.5		6.5	2.9		
Lower third/Fourth premolar															
LAET 75-778	7E	24.3	23.6	15.3	7.2	12.8	16.7	16.8	15.2	13.3	20.6	4.8	3.1	24.0	
LAET 75-804	7E	23.9		14.2	8.6	12.0	14.2		13.4	13.9					
LAET 75-905	7E	24.5	22.5	15.6	9.5	12.8	15.4	14.7	14.0	12.1	12.5	3.5	2.4	17.4	
EP 034/00	18	28.0	25.9	16.3	9.1	13.5	16.6	16.5	14.5	14.9	54.0	7.4	2.3	44.5	
LAET 75-2460	18	29.4		14.0	8.5	12.8	13.7		11.2	13.9					
Lower first molar															
LAET 75-1685	14	28.3	16.0	9.1	11.7	12.8	12.1	11.7	12.2	65.8			53.0		
LAET 78-4815	18	22.8		13.0	6.7	9.8	13.8		10.9	11.2	33.8	6.0	2.3		
Lower second molar															
EP 1210/03	7E	23.8	23.7	13.1	8.6	9.3	13.4	13.0	13.4	11.6	28.1	5.5	2.5	20.7	
EP 1211/03	7E	29.0		10.7	9.5	12.3		13.0	10.0	9.2	75.1			50.7	
LAET 76-3948	18	23.0	22.0	12.2	6.6	10.1	12.1	12.3	12.0	10.2	49.4	5.1	12.6	46.7	
LAET 78-4815	18	23.2	20.3	13.3	6.9	9.9	13.3		11.5	11.0	39.1	5.5	3.0	32.3	
Lower third molar															
LAET 78-5031	14	24.4	23.8	14.6	7.7	11.4	11.9	11.9		11.3	29.2	1.6	0.9	27.0	
LAET 78-4815	18	27.3	29.4	12.0	6.9	10.6	11.9	10.5	10.7	9.1	32.2	3.9	2.3	27.4	
Metacarpal III															
LAET 75-904	7E										36.2	32.4	31.5	25.1	28.2
EP 1208/03	7E										44.1	43.5	34.2	29.5	31.9
LAET 78-5095	7E										40.5	39.8	31.2	25.3	27.2
LAET 78-5027	14					45.0	30.9	39.1	13.0						
LAET 78-5036	14					45.4	29.0	37.2	13.3						
LAET 76-153	18										42.9	39.5	38.0	26.7	28.3
EP 926/00	18					44.1	29.4	38.6	10.8	6.5					
EP 927/00	18					42.1	29.0	36.0	11.8	5.1					
EP 976a/00	18										37.1	36.2	30.3	26.5	26.6
EP 976b/00	18										36.1	36.5	30.6	25.9	26.7
LAET 78-4857	18										39.0	35.3	30.7	27.7	28.7
EP 2352/00	18					44.5	31.3	37.5	12.8	7.6					
EP 1838/03	SA										51.6	51.7	39.5	31.1	33.4
Tibia															
LAET 75-927	7E							68.1	47.5						
LAET 75-930	7E			47.5	32.7			66.6	46.2						
LAET 75-1073	7E								44.5						

(continued)

Table 12.2 (continued)

Specimen	Loc	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
Calcaneus															
LAET 75-802	7E	112.2	73.7	20.5	33.5	51.3	54.5	54.3							
LAET 76-473	18	107.0	68.5	21.0	33.8	50.8	53.1	54.6							
Astragalus															
LAET 75-1640	14	66.7	64.2	31.7	66.3	52.5	38.6								
LAET 75-1659	14	56.9	59.0												
LAET 78-5056	14	57.2	55.1	29.8	54.8	45.6	32.2								
EP 083/03	18	56.4	57.4	26.7	54.5	47.4	38.2								
LAET 76-55	18	59.9	57.1	27.8	53.4	44.4	31.5	44.0							
Metatarsal															
LAET 75-903	7E										43.5	39.2	33.2	27.4	
LAET 75-904	7E											32.5	32.0	25.8	
LAET 75-928	7E					42.4	35.5	37.7	9.6						
LAET 75-2471	14	265.0	264.0	30.4	31.1	42.5	35.9	40.2			46.5	38.2	34.0	28.0	
EP 207/04	15										42.4	37.1	33.7	26.4	
EP 1687/03	15										41.5	40.0	32.3	25.9	
EP 157/76	18					43.8	35.2	42.1	8.8						
EP 284/76	18			28.22	26.48						43.74	41.53	37.14	28.1	
EP 286/76	18					47.5	37.5	42.7	13.3	4.8					
EP 357/76	18					39.3	31.8	37.9							
EP 1515/01	SA										42.9	39.4	34.6		
First phalanx (1 ph3)															
EP 163/76	7E				41.8	32.6									
LAET 75-800	7E	63.1	56.2	32.8	45.6	35.7	37.9	35.3	20.9	18.9	39.9	38.6	13.3	16.3	
LAET 75-1065	7E				45.8	37.5				18.8					
LAET 75-1077	7E				45.6	30.3									
EP 1493/00	7E	65.5	57.6	31.6	42.7	34.0	36.9	36.1	20.7	19.5	40.8	41.6	15.2	15.3	
LAET 75-2467	14	72.3	63.4	33.5	42.6	36.6	40.0	39.5	24.2	23.4	51.3	49.3	12.5	18.0	
EP 5030/75	14				39.9	32.2				10.6					
EP 208/76	18	64.2	60.0	28.5	39.8	31.4	34.5	34.0	22.0	19.0	44.9	45.3	12.5	11.8	
EP 084/03	18	63.6	56.7	30.5	42.4	33.7	36.8	35.5	20.1	9.9	49.8	50.0	11.4	12.3	
EP 3289/01	18	62.0	53.3	31.4	42.8	34.3	34.9	34.6	22.1	19.3	35.3	36.7	19.2	18.4	
EP 8418/03	18	63.8	58.0	30.1	42.4	32.9	36.5	35.5	21.2	18.4	40.1	39.7	16.7	17.3	
EP 1310/98	22S				43.5	34.8				23.5					

Table 12.3 Measurements (mm) of *Equus* sp. phalanges from Emboremony (EM, Ngaloba Beds) – (see text for explanation of measurements)

Specimen	Loc	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13
First phalanx (1 ph3)														
EP 367/99	EM	76.7	70.7	31.6	50.7	35.0	42.0	39.3	23.8	42.8	53.1	50.6	18.6	19.8
EP 2105/03	EM	78.4	69.1	33.3	53.8	37.4	43.9	39.0	20.3		52.3	54.9	17.3	14.4

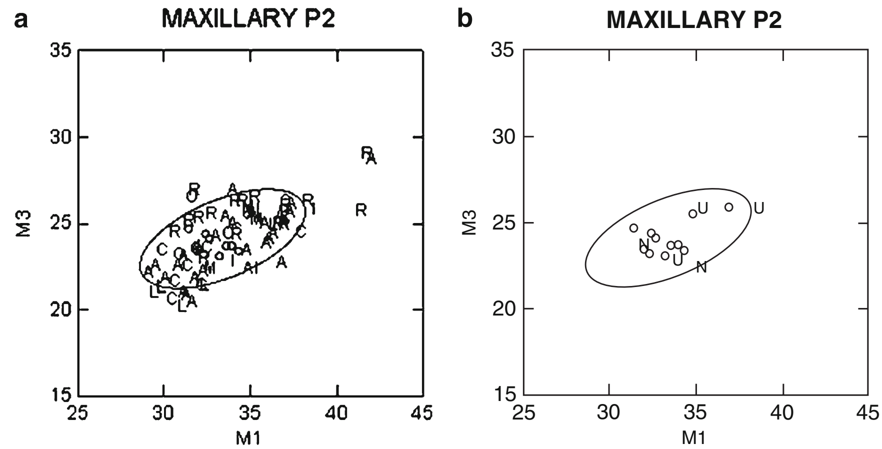

Fig. 12.1 (**a**) Bivariate plot of maxillary P2s occlusal width, (measurement M3) versus occlusal length (measurement M1) from the African hipparion sample plotted relative to the Eppelsheim ellipse (*A*=Middle Awash, *L*=Lothagam, *R*=Hadar). (**b**) Bivariate plot of maxillary P2s (occlusal width versus occlusal length) from the Upper Laetoli (*U*) and Upper Ndolanya Beds (*N*)

Calcanea

Figure 12.2a plots calcaneal maximum length (M1) versus maximum width (M6) for our sample compared to the Höwenegg 95% confidence ellipse. All but one of the Laetoli (I) specimens fall either within, or immediately outside the ellipse; Hadar specimens (R) plot at the upper border, or above the Höwenegg ellipse; Langebaanweg, C, plots at the bottom, or below the Höwenegg ellipse. One Laetoli specimen falls very far below the ellipse and is a smaller form. Figure 12.2b plots the Laetoli specimens by horizon, the two Upper Ndolanya Bed specimens fall within the ellipse, the Upper Laetolil Bed specimen at the upper limit of the ellipse and a single specimen falls well below the ellipse.

Astragali

Astragali are usually far more common than calcanea in collections, and this is reflected in our sample plotted in Fig. 12.3. In our larger sample (Fig. 12.3a) we find that astragali vary in size far beyond the range represented by Höwenegg 95% confidence ellipse of *Hippotherium primigenium*. This plot shows a number of larger astragali specimens from Hadar (R) and Laetoli (I), some from Awash (A) and Olduvai (O) and smaller specimens from Olduvai, Lothagam (L), Langebaanweg (C) and Omo (G). The large specimens from Hadar are referable to *Eurygnathohippus hasumense* (*sensu* Bernor et al. 2005), and those from Awash are perhaps *Eu.* aff. *turkanense*. Small taxa have been reported from Lothagam (*Eu. feibeli*, Bernor and Harris 2003), Olduvai and Omo (Armour-Chelu et al. 2006). The Olduvai specimen far to the right of the ellipse may be referable to *Equus oldowayensis*, having a wide distal facet (re Gilbert and Bernor 2008). Figure 12.3b plots the Laetoli specimens by horizon and here we find that the Upper Ndolanya specimens mostly fall within the ellipse, while most of the Upper Laetolil Beds specimens fall either above or to the left of the ellipse. This suggests that the dominant morph (and potentially species) in the Upper Ndolanya Beds is smaller (the size of the Höwenegg species), while the Upper Laetolil sample may include more than a single species, one large and the other small. The larger Laetoli form overlaps extensively in size with the Hadar hipparion and could be referable to *Eurygnathohippus* cf. *hasumense* as found in the Beredi Member of the Manonga Valley fauna in Tanzania, (Bernor and Armour-Chelu 1997). We further plotted, but do not figure here, distal articular facet depth (M6) versus width (M5) and this analysis exhibits very much the same result as illustrated in Figs. 12.3a and b.

Metacarpal III

There are no complete hipparion MCIIIs in the Laetoli sample available to us. In Fig. 12.4a we provide a broad sample of complete MCIIIs plotting maximum length (M1) versus distal articular width (M11) exhibiting the great variation in size of African hipparions compared to the Höwenegg population. Most remarkable are the extremely long MCIIIs from Hadar (R) and the extremely small specimen from Sahabi (Bernor and Scott 2003; Bernor et al. 2008); the large Olduvai specimens to the far right of the ellipse are likely *Equus* cf. oldowayensis (Gilbert and Bernor 2008). Fig. 12.4b is a similarly large sample of MCIII measurements

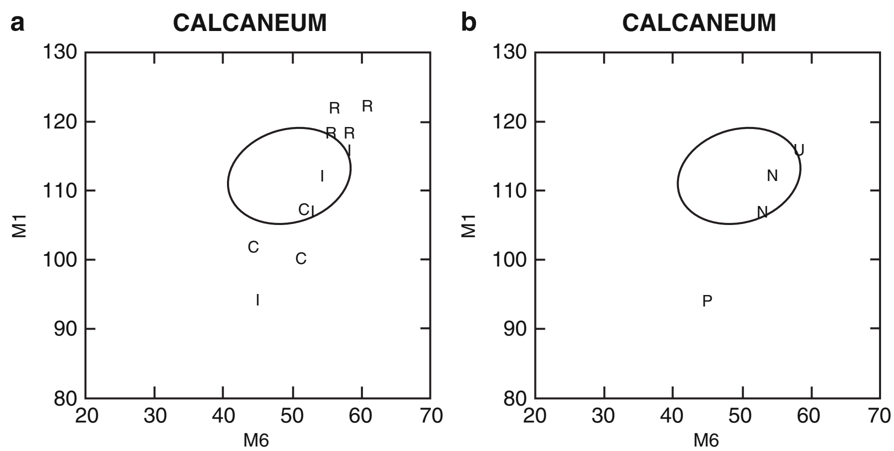

Fig. 12.2 (**a**) Bivariate plot of calcaneum from Laetoli (*I*), Hadar (*R*) and Langebaanweg (*C*) (maximum length vs maximum width) relative to the Höwenegg ellipse. (**b**) Bivariate plot of calcaneum (maximum length vs maximum width) from the Upper Laetolil (*U*) and Upper Ndolanya Beds (*N*) relative to the Höwenegg ellipse

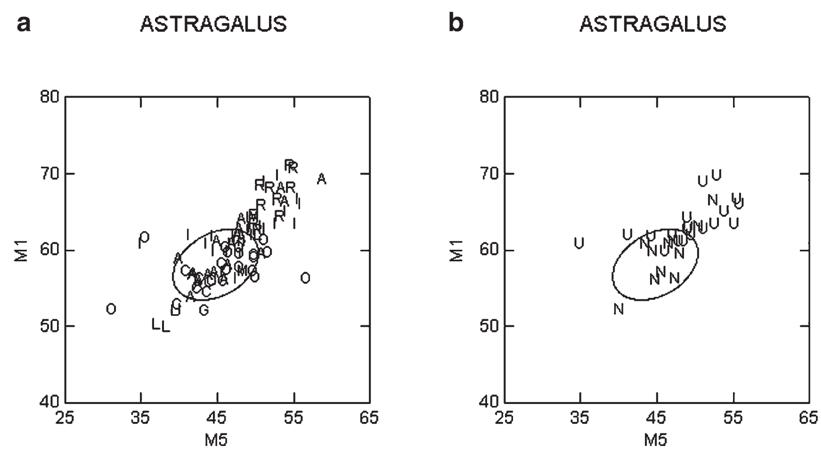

Fig. 12.3 (**a**) Bivariate plot of astragali maximal length (measurement M1) versus distal articular width (measurement M5) from the African hipparion sample plotted relative to the Höwenegg ellipse. (**b**) Bivariate plot of astragali maximal length (measurement M1) versus distal articular width, (measurement M5) from the Upper Laetolil (*U*) and Upper Ndolanya Beds (*N*) plotted relative to the Höwenegg ellipse

on proximal articular depth (M6) versus proximal articular width (M5): most Laetoli specimens plot at the upper limit, or somewhat above the Höwenegg ellipse, while Hadar and Olduvai specimens fall much further above the ellipse; specimens within the ellipse include those from Olduvai (O), Langebaanweg (C), Manonga Valley (M), Lothagam (L; likely *Eurygnathohippus feibeli*) and Middle Awash (A; also likely *Eurygnathohippus feibeli*). The Hadar specimens have greater proximal width dimensions than the Upper Laetolil specimens with the former being referable to *Eu. hasumense*. The same can be said for the large and very broad Olduvai specimens, which are most likely referable to *Equus oldowayensis*. The smaller Laetoli specimens are from the Upper Ndolanya Beds and overlap extensively with some of the Olduvai specimens. Referring back to Fig. 12.4b, it can be seen that Olduvai specimens show the greatest variation in size of all sites and this undoubtedly indicates multiple equid taxa, which certainly include species of *Equus* and *Eurygnathohippus.*

Figure 12.4c plots Laetoli proximal MCIIIs by horizon: the Upper Ndolanya specimens plot at the upper extreme and above the Höwenegg ellipse while the Upper Laetolil Beds specimens overlap slightly and are larger than the Upper Ndolanya specimens. Figure 12.4d plots a large sample of distal MCIII specimens distal sagittal keel (M12) versus distal articular width (M11); this graph exhibits that great range of variability among taxa under consideration and the extreme development of the distal sagittal keel, most prominent in the Hadar (R) *Eurygnathohippus hasumense* sample (Bernor et al. 2005). Figure 12.4e plots the Laetoli specimens by stratigraphic unit and includes substantial diversity in the Upper Ndolanya sample, which may well represent more than one taxon and specimens from the Upper Laetolil Beds and unknown provenance to the right and above the Höwenegg ellipse.

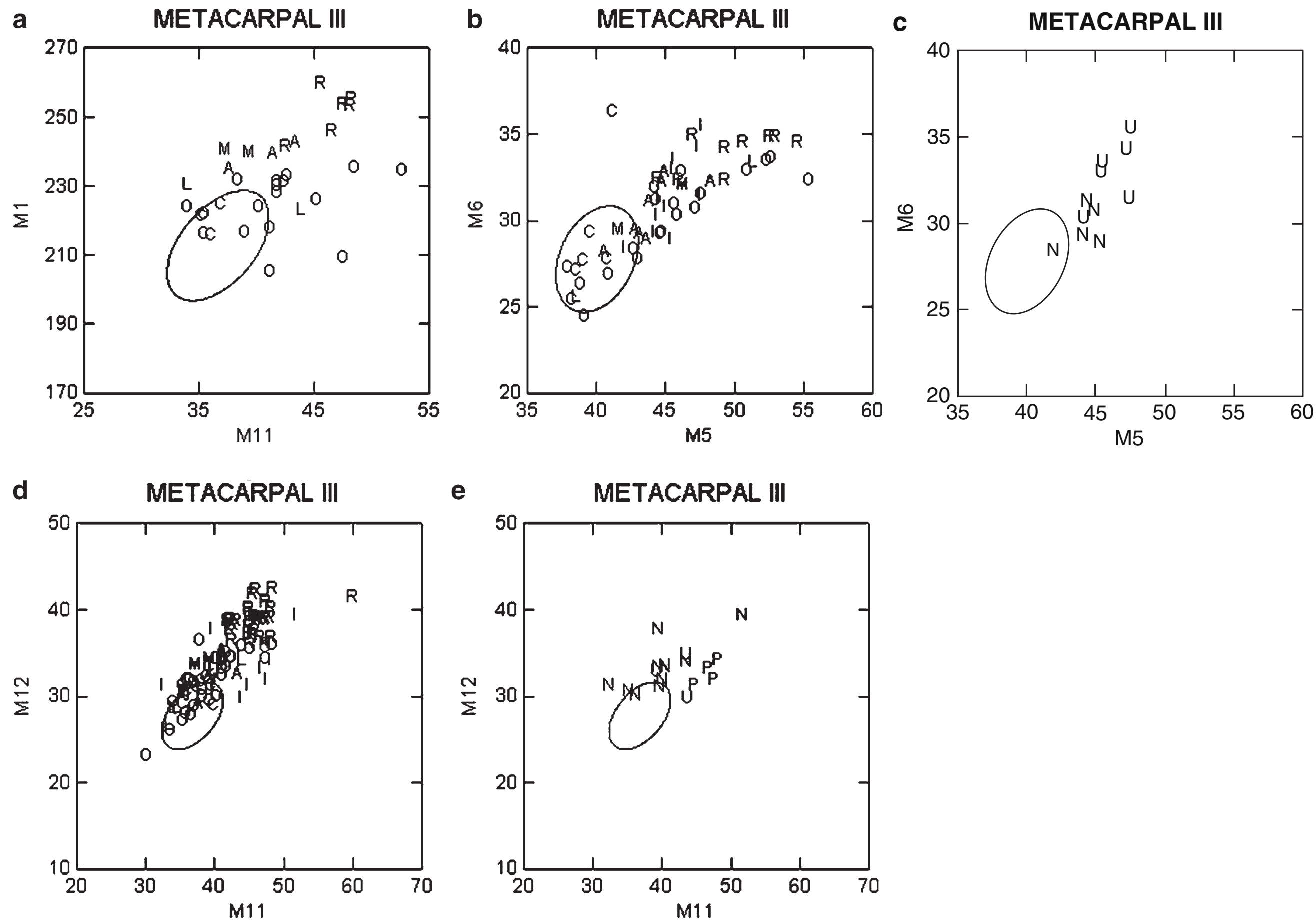

Fig. 12.4 (**a**) Bivariate plot of complete MCIII from the African sample, plotting maximum length (M1) versus distal articular length (M11) compared to the Höwenegg ellipse. (**b**) Bivariate plot of proximal articular width (M5) versus proximal articular depth (M6), showing Laetoli specimens relative to Höwenegg ellipse and the African sample. (**c**) Bivariate plot of proximal articular width (M5) versus proximal articular depth (M6) plotted by horizon and compared to the Höwenegg ellipse. (**d**) Bivariate plot of distal articular width (M11) versus sagittal keel (M12) of African sample of distal MCIIIs. (**e**) Bivariate plot of distal articular width (M11) versus sagittal keel (M12) of Laetoli specimens plotted by stratigraphic unit

Metatarsal III

Figure 12.5a is a bivariate plot of MT III length (M1) versus width (M11) comparing a large sample of African specimens to the Höwenegg sample. The majority of specimens are derived from Olduvai, most of which plot within the Höwenegg ellipse, but with some smaller and larger specimens. Langebaanweg *Eurygnathohippus hooijeri* (Bernor and Kaiser 2006) overlaps with the Höwenegg population, being at the top or above its range. Middle Awash specimens plot just to the right or above the ellipse being somewhat larger than the Höwenegg population. The largest MT III is derived from Hadar *Eurygnathohippus hasumense* (Bernor et al. 2005). The single Laetoli specimen (I), plotting slightly above the ellipse, is from the Upper Ndolanya Beds (Fig. 12.5b), and overlapping with the intermediate range of the Olduvai specimens. Figure 12.5c represents a large sample of African proximal MT IIIs for which we plot proximal articular depth (M6) versus width (M5). Significant features here include: most of the Olduvai specimens plot within the ellipse, but there is a significant dispersion of specimens above and to the left of the ellipse as well as just above the ellipse, likely indicative of at least two hipparionine taxa; Hadar *Eurygnathohippus hasumense* (R) again plots well above the ellipse overlapping with the massively built Lothagam *Eurygnathohippus turkanense* (L). Figure 12.5d plots the Laetoli sample by horizon and all specimens from the Upper Ndolanya Beds (five from N), Lower Laetolil Beds (one from L) and uncertain provenance (one from P) plot within the Höwenegg ellipse. Figure 12.5e is important documentation of the significant increase in MT III distal sagittal keel dimensions in African hipparions, with Hadar (R) being the most prominent. Figure 12.5f plots the Laetoli sample by horizon: most Upper Ndolanya specimens plot within or just outside the ellipse (mostly above indicating increased M12 dimension), with a few specimens plotting above the ellipse from the Upper Ndolanya, Upper Laetolil, Lower Laetolil and unknown provenance.

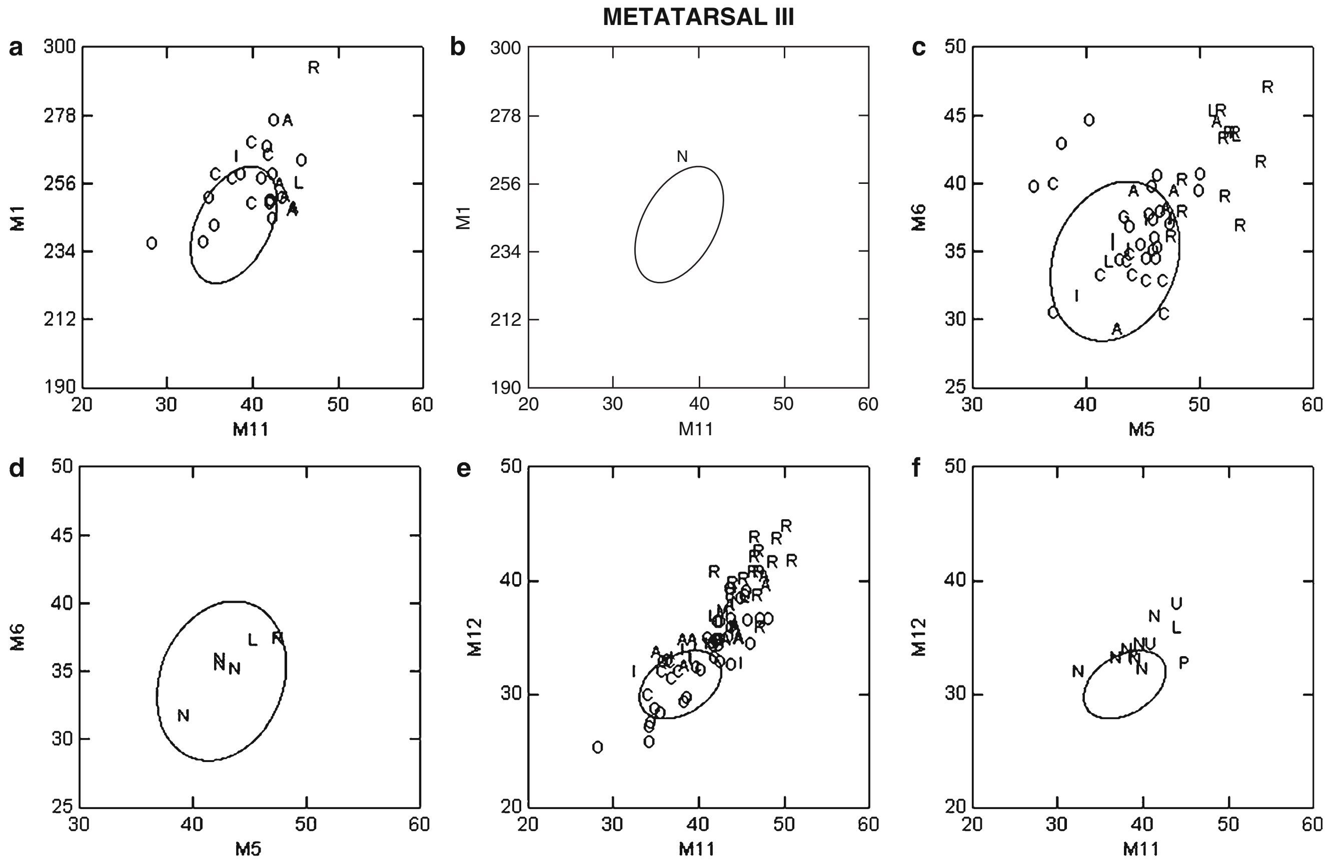

Fig. 12.5 (**a**) Bivariate plot of MTIII maximum length (M1) versus distal width (MII) of African sample compared with the Höwenegg ellipse. (**b**) Bivariate plot of MTIII maximum length (M1) versus distal width (M11) of complete MTIII from Upper Ndolanya Beds. (**c**) Bivariate plot of MTIII proximal articular width (M5) versus proximal articular depth (M6) from the African sample compared to the Höwenegg ellipse. (**d**) Bivariate plot of MTIII proximal articular width (M5) versus proximal articular depth (M6) from the Laetoli sample by horizon compared with the Höwenegg ellipse. (**e**) Bivariate plot of MTIII distal sagittal keel dimension, (M11 – distal maximal articular width) versus M12 (distal maximal depth of the keel) in the African sample. (**f**) Bivariate plot of MTIII distal sagittal keel dimensions from Laetoli plotted by horizon (distal maximal articular width M11 versus distal maximal depth of the keel M12)

We calculated a number of MT III log10 ratio plots all using the mean Höwenegg log10 standard. Figure 12.6a compares the Höwenegg standard to the mean Sinap *Cormohipparion sinapensis* sample (Turkey; AS_Mean2; Bernor et al. 2003), the Langebaanweg sample (South Africa; SAM_Mean2; Bernor and Kaiser 2006), Daka (Ethiopia; BOU-VP-26/13) *Eu.* aff. *cornelianus* (Gilbert and Bernor 2008), Olduvai *Eu. cornelianus* (Armour-Chelu et al. 2006) and the Upper Ndolanya specimen EP 75-2471R. The Sinap mean is believed to represent the primitive condition for Old World hipparions (Bernor et al. 2003; Bernor and White 2009) with particular regard to: its length (M1) is only slightly less than the Höwenegg mean, its mid-shaft width (M3) is very narrow and its depth slightly less than Höwenegg; other dimensions are less, reflecting slighter build than the Höwenegg hipparion. The Langebaanweg specimen is longer (M1) than in the Höwenegg sample, but a mid-shaft width (M3) versus mid-shaft depth (M4) proportion is virtually identical to Daka *Eu.* aff. *cornelianus*. The remainder of Langebaanweg's dimensions is similar to *H. primigenium*. The Laetoli MT III most closely compares with Olduvai *Eu. cornelianus* and the Daka hipparion, except for M11 (distal articular width), which is lower and overlaps with Langebaanweg. The close comparison of the Upper Ndolanya MT III dimensions to Olduvai and Daka hipparions supports Armour-Chelu et al.'s (2006) observation that the *Eu. cornelianus* lineage extends back to Upper Ndolanya horizons at 2.66 Ma.

Figure 12.6b compares the Laetoli MT III (EP75-2471) with samples from Hadar (AL 155-6AZ), Olduvai (OLDEoldMEAN), Ahl al Oughlam, Morocco (AaOMTIII Mean) and Sinap (AS_Mean2). This plot clearly shows the dramatically different dimensions and larger size of Olduvai *Equus oldowayensis* (OLDEoldMEAN) compared to all hipparions considered (Gilbert and Bernor 2008); M1 is relatively short, midshaft width (M3), midshaft depth (M4), proximal articular width and depth (M5 and M6) and distal dimensions (M11, M12 and M13) are greatly elevated compared to all other hipparions, except *Eu. hasumense* for M11, M12 and M13. The Hadar *Eurygnathohippus hasumense* metatarsal has the greatest overall length (M1) and midshaft width (M3)

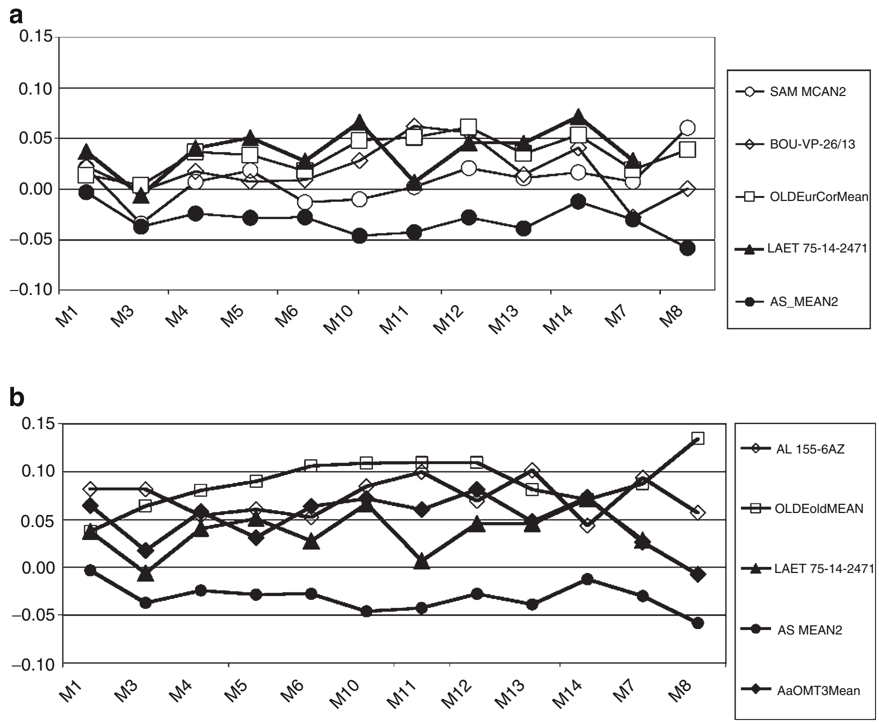

Fig. 12.6 (**a**) Metatarsal III log10 ratio diagram (Höwenegg Standard) showing more slender limbed equids from Langebaanweg, Daka, Olduvai, Laetoli and Sinap. (**b**) Metatarsal III log10 ratio, Hp. Std., larger equids from Olduvai, Hadar and Ahl al Oughlam (AaO) compared to primitive *Cormohipparion sinapensis* and Laetoli Upper Ndolanya Beds

followed by the Moroccan MTIII (*Eurynathohippus pomeli*). While the Moroccan *Eurygnathohippus pomeli* metatarsals (Eisenmann and Geraads 2007; Bernor et al. 2010) are clearly longer than the Laetoli specimen, the proportions for most dimensions (except M11) track the Laetoli specimen quite closely and, on face value, suggest a possible evolutionary relationship. The possibility that *Eu. pomeli* and *Eu. cornelianus* are sister taxa is an observation contrary to Eisenmann and Geraad's (2007) recent interpretations.

First Phalanges III

We undertook a number of bivariate calculations and have found the maximum length (M1) versus proximal articular width (M4) is the most useful (Fig. 12.7). Figure 12.7a exhibits the major increase in length of first phalanges in several African hipparions, and in particular the Hadar hipparions (R). Lothagam (L), Langebaanweg (C), Middle Awash (A), Laetoli (I) all have several specimens plotting within the Höwenegg ellipse and as such are conservative in their morphology. Figure 12.7b plots the Laetoli specimens by stratigraphic horizon: most of the Upper Ndolanya specimens fall within the Höwenegg ellipse (six within, only one above), whereas the Upper Laetolil Beds specimens plot just outside the ellipse. Figure 12.8a is a log10 ratio plot of 1PH III Laetoli *Eurygnathohippus* aff. *cornelianus* (mean) compared to Daka *Eurygnathohippus* aff. *cornelianus* (BOU-VP-12/89; Gilbert and Bernor 2008), Hadar *Eurygnathohippus hasumense* (AL155-6X; Bernor et al. 2005), Lothagam *Eurygnathohippus turkanense* (mean; LTEurturkMean; Bernor and Harris 2003) and Langebaanweg *Eurygnathohippus hooijeri* (mean; SAM_MEAN2; Bernor and Kaiser 2006). The log10 ratio profile of the Laetoli mean is virtually identical to that of the Daka 1PH III (BOU-VP-12/89), supporting our conclusion that they are both members of the *Eurygnathohippus cornelianus* lineage.

Eurygnathohippus hooijeri (SAM_Mean2) is virtually identical to the Daka specimen, except for the slightly elevated maximum length measurement, which is more like the Laetoli EuMean. Hadar *Eurygnathohippus hasumense* is a larger form being the longest of all the sampled 1PH III. Lothagam *Eurygnathohippus turkanense* 1PH III is no longer than the comparative sample, but has a midshaft width (M3), proximal width (M4), depth (M5) and distal articular width measurement virtually identical to *Eu. hasumense*: it is a relatively short, massively built 1PH III. Overall, this plot shows the similarities in the proportions of the Laetoli, Daka and Langebaanweg samples.

Figure 12.8b compares individual specimens of Laetoli *Eurygnathohippus* aff. *cornelianus* first phalanges with the mean of Laetoli *Eu.* aff. *cornelianus*, Daka *Eu.* aff. *cornelianus*, Langebaanweg *Eu. hooijeri* and Laetoli *Equus*. These plots exhibit the striking intrapopulation similarity of all Laetoli

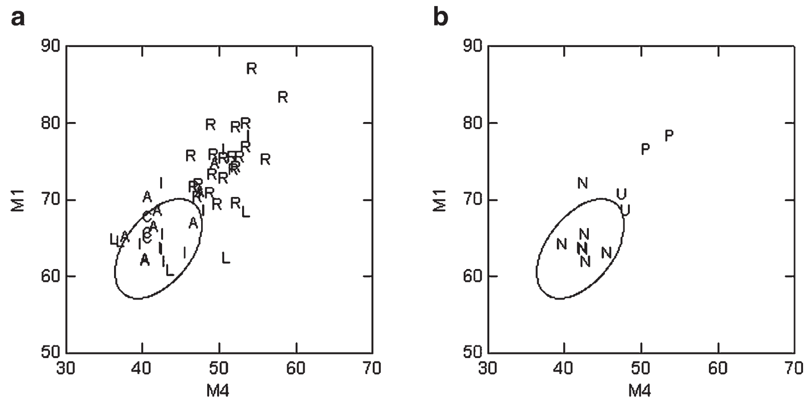

Fig. 12.7 (**a**) Bivariate plot of maximum length (M1) of 1PHIII versus proximal articular width (M4) in African hipparion sample plotted with the Höwenegg ellipse. (**b**) Bivariate plot of maximum length (M1) of 1PHIII versus proximal articular width (M4) in Laetoli sample plotted with the Höwenegg ellipse

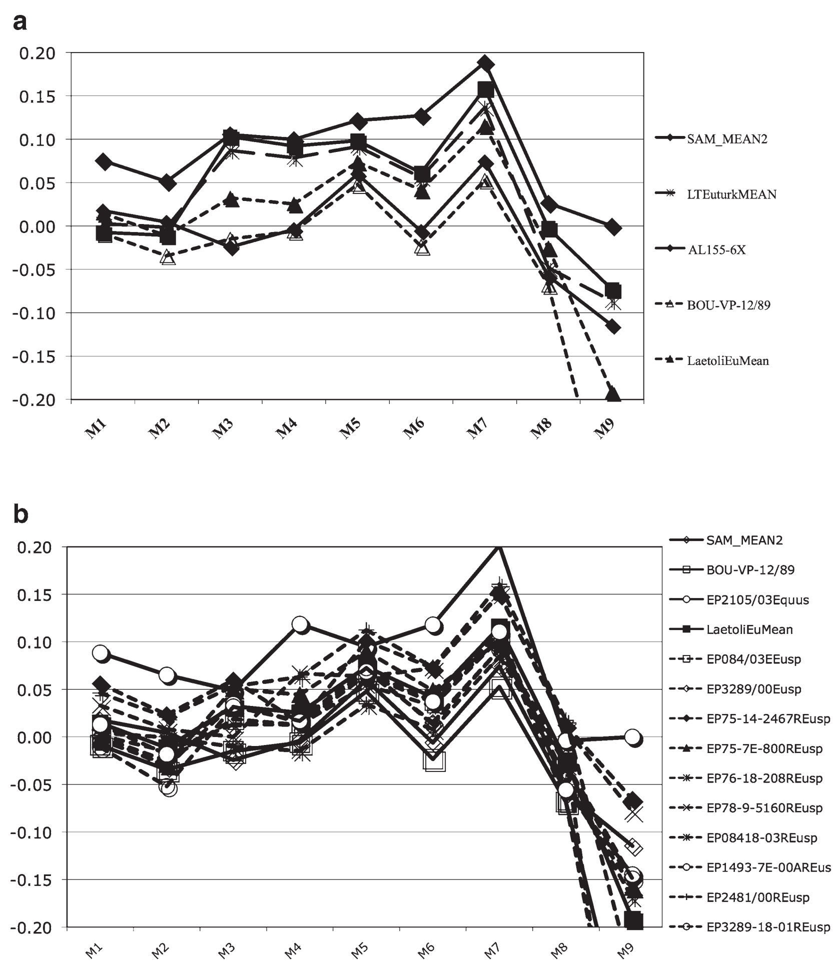

Fig. 12.8 (**a**) Comparison of Laetoli, Langebaanweg, Hadar and Daka *Eurynathohippus* 1 PHIII's (Höwenegg Std.). (**b**) Comparison of Langebaanweg, Daka, Laetoli *Eurynathohippus* aff. *cornelianus* with Laetoli 1PHIII, (Höwenegg Std.)

Eu. aff. *cornelianus,* the close resemblance of Daka *Eu*. aff. *cornelianus* to this sample (albeit at the smaller size of the range), the similar line profile of *Eu. hooijeri* to *Eu.* aff. *cornelianus,* the distinct morphology of Laetoli *Equus* 1PH III, particularly the higher values of maximum length (M1), proximal articular width and distal width measurements (M6 and M7).

Summary of Metrical Results

This analysis supports the conclusion that there are likely three equids from Laetoli: an Upper Laetolil Beds hipparion, which is larger than the Upper Ndolanya Beds form, and *Equus* is identified from Emboremony 2 (Ngaloba Beds). The results from P2 (Fig. 12.1) generally show a great size distribution but, in itself, is not conclusive. The calcanea plots (Fig. 12.2) revealed how much larger the Hadar *Eu. hasumense* was compared to the rest of the hipparion sample. The astragali bivariate plots (Fig. 12.3) revealed larger individuals from the Upper Laetoli Beds and smaller ones, plotting mostly within the Höwenegg ellipse, from the Upper Ndolanya beds. There were no complete MC IIIs from Laetoli, but analyses on proximal articular depth (M6) versus width (M5) dimensions revealed that the Upper Ndolanya beds specimen overlapped the Höwenegg ellipse and intermediate sized Olduvai specimens. Our analysis of MT III bivariate (Fig. 12.5) revealed much the same thing. Our log10 ratio analysis on MT IIIs (Fig. 12.6) revealed that the Laetoli sample was distinct from Olduvai *Equus oldowayensis*, Hadar *Eurygnathohippus hasumense* and is closest in its proportions to Moroccan *Eurygnathohippus pomeli*. The 1PH IIIs again revealed that the Hadar hipparion is distinct in its large size, the Upper Ndolanya Beds hipparion are similar in size to Höwenegg *Hippotherium primigenium*, while the Upper Laetolil Beds specimens are somewhat larger. The 1PH III log 10 ratio diagrams we present here (Figs. 12.8a, and b) overall reveal the close identity of Upper Ndolanya Beds, Daka and Langebaanweg samples. We suggest here that *Eu. pomeli* is possibly the sister taxon of the *Eu. cornelianus* lineage and, these may be related to Langebaanweg *Eurygnathohippus hooijeri* (Bernor and Kaiser 2006).

Description of the Material

Maxillary Teeth

Upper Laetolil Beds

There are a number of maxillary teeth that we have measured and photographed from the Upper Laetolil Beds and we discuss representative samples serially.

LAET 75-1430 is a right P3 with a mesostyle height of 58.1 mm (Fig. 12.9a, b). The labial view (Fig. 12.9a) has the characteristic mesialward slant of a P3, has strongly developed parastyle and mesostyle and both the mesial and distal ectoloph enamel bands are worn blunt, indicative of a diet that was predominantly graze. Occlusally (Fig. 12.9b), there are the following salient features: parastyle is pointed labialward

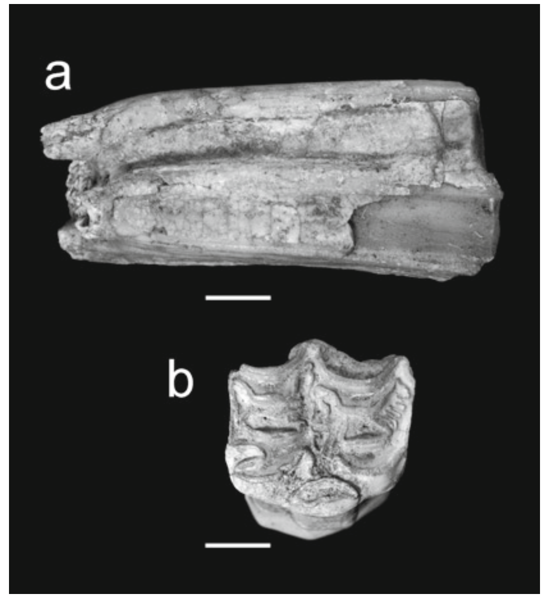

Fig. 12.9 (**a**) LAET 75-1430 rt P3 (*labial* view). (**b**) LAET 75-1430 rt P3 (*occlusal* view). Scale = 1 cm

while mesostyle is squared labialward; fossette plications are complex on the mesial and distal borders of the prefossette and the mesial wall of the postfossette, only; pli caballins are double, protocone is elongate, flattened lingually and rounded labially; hypoglyph is deeply incised.

EP 1494/98 (Fig. 12.10a, b) is a right P4 that is in wear and has a 60.5 mm crown height. Figure 12.10a is a labial view that shows the prominent parastyle and mesostyle. The enamel band ectoloph is absolutely flat mesially, low and rounded distally, suggesting that the individual had a diet that was predominantly composed of graze. Figure 12.10b has an occlusal surface that is worn, but not yet in middle wear, yet the following salient features can be identified: parastyle and mesostyle have pointed aspects labialward; the distal border of the prefossette and mesial border of the postfossette are complex, while their opposing borders are simple; pli caballin is clearly double, protocone is flattened, elongate and is rounded labially and flattened lingually; the hypoglyph is very deeply incised.

LAET 75-2070 is a left M1, in relatively early wear with a mesostyle crown height of 64.4 mm. Figure 12.11a is a labial view that reveals the slight backward slant of an M1 and a mesial ectoloph that is flat and a distal ectoloph that is low and rounded; the wear pattern is typical of a grazer. The occlusal view (Fig. 12.11b) reveals an eroded crown surface with the following salient features: labially squared parastyle and mesostyle; pre- and postfossettes in too early wear to adequately express their plication frequency; pli caballin not preserved; protocone elongate with labially rounded and lingually flattened surfaces; hypoglyph only moderately incised.

LAET 75-3532 is a right M2 that has a mesostyle crown height of 60.2 mm. The labial view (Fig. 12.12a) exhibits the

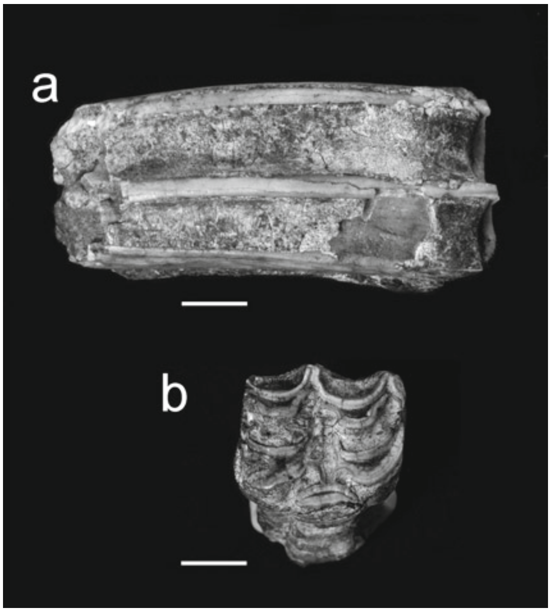

Fig. 12.10 (**a**) EP 1494-98, rt P4 (*labial* view). (**b**) EP 1494-98, rt P4 (*occlusal* view). Scale = 1 cm

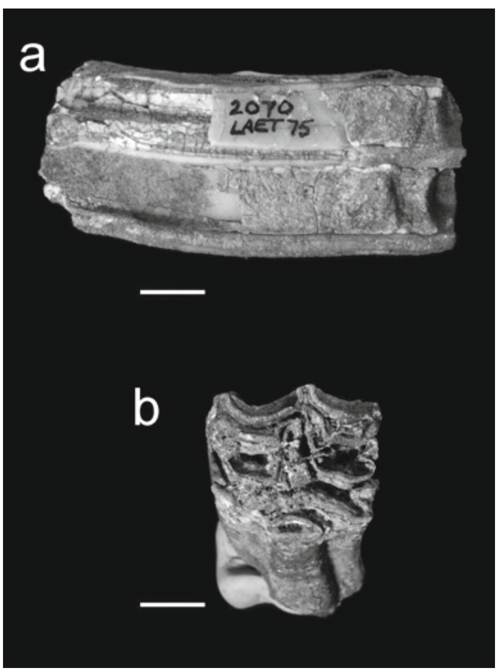

Fig. 12.11 (**a**) LAET 75-2070, lt M1 (*labial* view). (**b**) LAET 75-2070, lt M1 (*occlusal* view). Scale = 1 cm

sharp distalward slant typical of the M2 and the ectoloph is worn low and flat mesially and is low and rounded distally. The occlusal surface (Fig. 12.12b) is well worn and exhibits the following salient features: parastyle is pointed labialward while mesostyle is squared labialward; both the mesial and distal borders of the prefossette are complex while on the mesial border of the postfossette is complex; pli caballin is

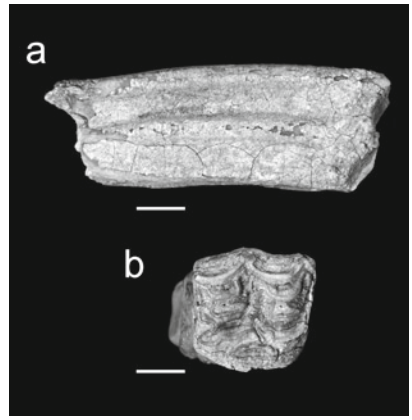

Fig. 12.12 (**a**) LAET 75-3532, rt M2 (*labial* view). (**b**) LAET 75-3532, rt M2 (*occlusal* view). Scale = 1 cm

Fig. 12.13 (**a**) EP 502/01, lt M3 (*labial* view). (**b**) EP 502/01 lt M3 (*occlusal* view). Scale = 1 cm

large, but single; hypoglyph is moderately deeply incised; protocone is as in the other maxillary dentition described thus far being elongate with a rounded labial and flattened mesial surface.

EP 502/01 is a left M3 with a mesostyle height of 60.1 mm. Figure 12.13a exhibits the characteristically sharp distalward curvature typical of an M3, the ectoloph mesial enamel band is low and rounded while the distal one is virtually flat as is found in grazers. The occlusal surface (Fig. 12.13b) exhibits essentially the same morphology as is found in other specimens from the Upper Laetolil Beds: parastyle pointed and mesostyle squared labially; the prefossette mesial and distal borders are complex as is the mesial border of the postfossette; pli caballin is weakly double; protocone is elongate being rounded labially and flattened distally; hypoglyph is deeply incised.

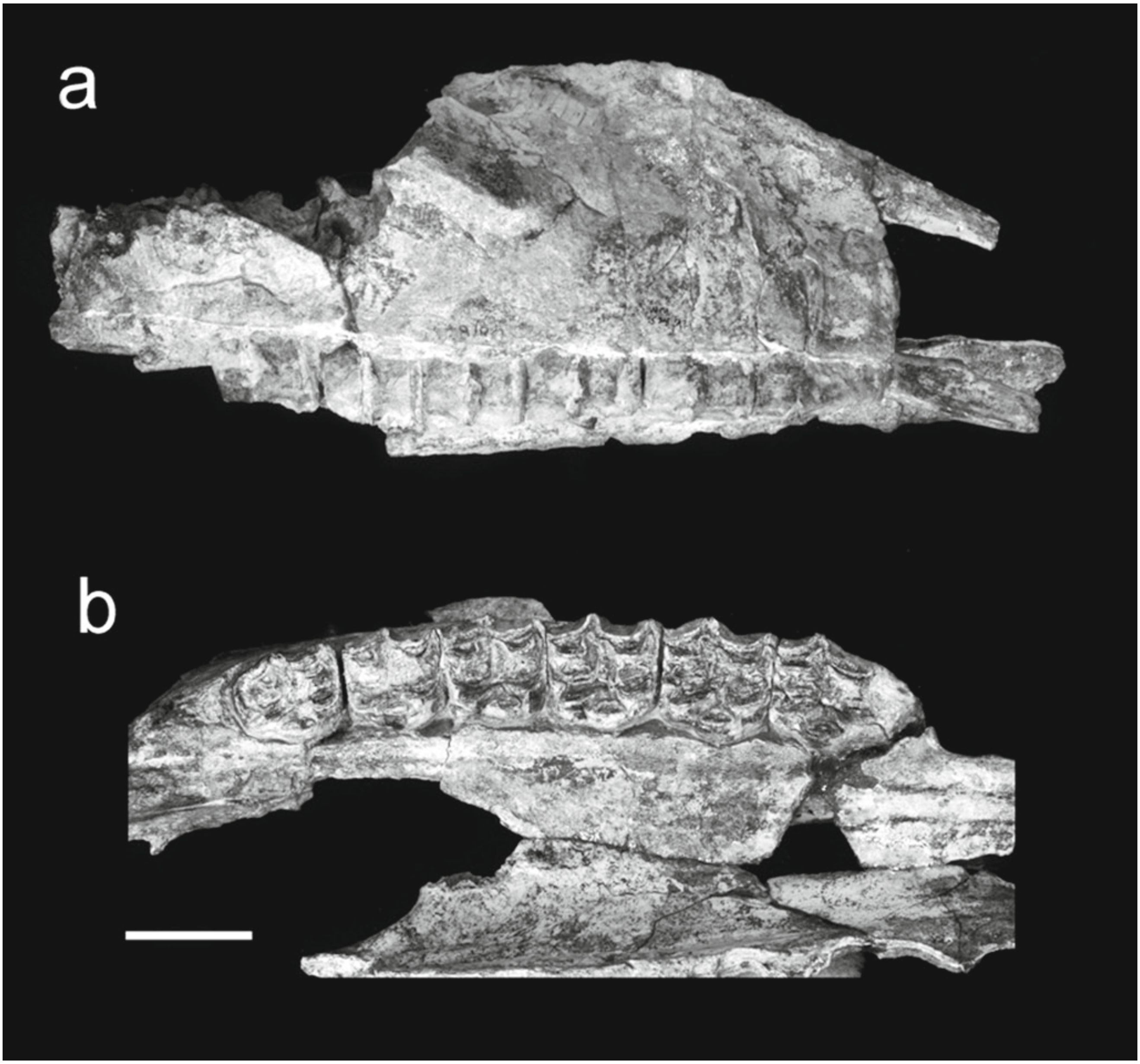

Fig. 12.14 (**a**) WM 1528/92, Beredi 3, Manonga Valley. Lateral view of skull. (**b**) WM 1528/92, Beredi 3, Manonga Valley. *Occlusal* view of P2-M3. Scale = 3 cm

For comparison with the Upper Laetolil Beds, we illustrate here the Beredi 3 skull. Figure 12.14a is a lateral view of WM 1528/92. As with the Upper Laetolil Beds cheek teeth the ectoloph cusps are either flat, low and rounded, or as in the mesial portion of M3 ectoloph actually concave. This morphology is indicative of grazing. Figure 12.14b provides a close-up view of the P2-M3 occlusal surfaces. The poor contrast of this specimen does not allow occlusal details to be exhibited, but the morphology of parastyle, mesostyle, fossettes, pli caballin, protocone and hypocone is essentially identical to the Upper Laetolil Beds hipparion and is undoubtedly closely related or conspecific with that taxon.

Upper Ndolanya Beds

LAET 75-3793 is a left maxillary I3 that is well worn. Both the labial (Fig. 12.15a) and lingual views (Fig. 12.15b) reveal a mesiodistally long (31.2 mm) dimension, with strong lingual grooving and a distinct distal taper. The tooth is derived for a *Eurygnathohippus*, but does not seem as derived as Olduvai Bed II *Eu. cornelianus.*

LAET 75-2458 is an unworn left P2 that preserves too little morphology to warrant description or figuring. There is a worn associated P2 and P3, LAET 78-4872 from Loc. 18, Upper Ndolanya Beds. There are two P4s, EP 986/00 from Loc. 18

Fig. 12.15 (**a**) LAET 75-3793, lt I3 (*labial* view). (**b**) LAET 75-3793, lt I3 (*lingual* view). Scale = 1 cm

Fig. 12.16 LAET 75-1685 lt M1 (*occlusal* view). Scale = 1 cm

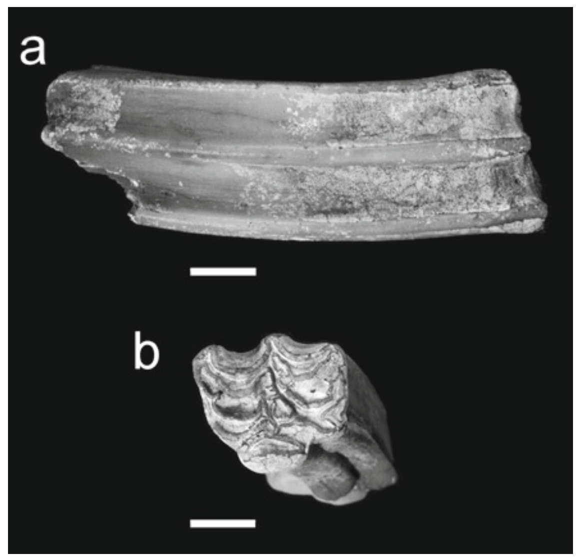

Fig. 12.17 (**a**) LAET 75-1685, lt M2 (*labial* view). (**b**) LAET 75-1685, lt M2 (*occlusal* view). Scale = 1 cm

and EP 1213/03 from Loc. 7E which are too worn for description. A rolled and damaged M1, EP 4008/00 is known from the Upper Ndolanya Beds. The specimen is too damaged to obtain an accurate crown height, but enough is present to state that it is an adult tooth, well in wear with fossette morphology and protocone shape as in other Upper Ndolanya Bed specimens.

There is an associated tooth row LAET 75-1685 from Loc. 14, Upper Ndolanya Beds, comprising left M1, M2, and right M1, M2. These teeth were described by Hooijer (1987b). The teeth are in early to middle wear, they are associated with a lower cheek tooth, (left m1), which by its state of preservation and stage of wear would likely be from the same individual. The left M1 with a mesostyle crown height of 75.0 mm, is the best preserved. As shown in Fig. 12.16, the tooth is well worn despite its relatively high crown height preserving the following salient features: parastyle is pointed labialward while mesostyle is narrow but squared labialward; both the mesial and distal surfaces of the prefossette are complex, while in the postfossette only the mesial side is complex. The pli caballin is single, hypoglyph is deeply incised and protocone is elongate, labially rounded and lingually flattened. The protocone of the left M^1 measures 10 mm anteroposteriorly and 4 mm transversely. The M2 (left) LAET 75-1685 has a mesostyle crown height of 75.3 mm. The labial view (Fig. 12.17a) reveals the strong distal curvature of the tooth, typical for an M2, and the low rounded (mesially) and flat (=blunt, distally) ectoloph enamel band. The occlusal surface is in early wear but reveals some occlusal ornamentation (Fig. 12.17b): the fossettes are not well developed, but the opposing borders of the pre- and postfossette have rich plications coming into wear; the pli caballin is single; hypoglyph is moderately deeply to deeply incised, protocone is elongate, rounded labially and flattened lingually.

The Upper Ndolanya Beds hipparion upper cheek teeth exhibit a number of similarities with the Upper Laetolil Beds although they differ in crown height: the Upper Ndolanya Beds have a higher maximum crown height, which we estimate as being 80 mm (compared to 70 mm in the Upper Laetolil Beds). In this regard, the Upper Ndolanya Beds hipparion resembles the Olduvai species *Eurygnathohippus cornelianus*.

Mandibular Cheek Teeth

Lower Laetolil Beds

There are two mandibular cheek teeth from the Lower Laetolil Beds: EP 035/98 (Fig. 12.18), a left dp4 and EP 032/98 a left p4. Both only preserve the occlusal surfaces well. The dp4 (Fig. 12.18a) is elongate, has a rounded metaconid and distally pointed metastylid, the pre- and postflexids have simple margins, the linguaflexid is broad and the deep protoconid has a flattened enamel band labially and there is a very small, pointed ectostylid. The p4 occlusal surface is well preserved and has a rounded metaconid, distally pointed metastylid; linguaflexid is a deep V-shape, preflexid has relatively simple margins while the postflexid has more complicated margins, pli caballinid is distinct, ectostylid is a distinctly rounded feature on the labial margin of the tooth (Fig. 12.18b).

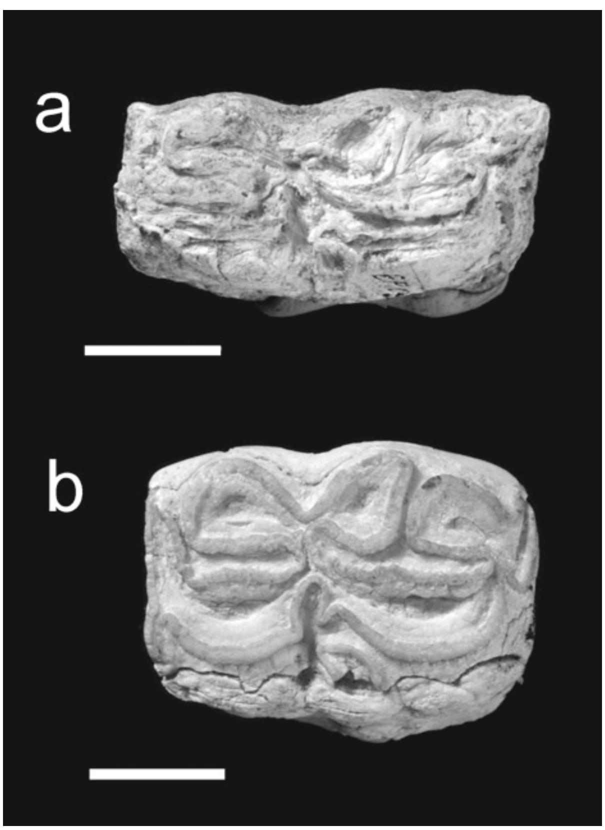

Fig. 12.18 (**a**) EP 035/98, lt dp4 (*occlusal* view). (**b**) EP 032/98, lt p4 (*occlusal* view). Scale = 1 cm

Upper Laetolil Beds

EP 363/98 is a right i2 and i3 from the same individual, extremely worn and in poor condition. The crown height of i2 is 18 mm to the cementum-enamel junction and 12 mm transversely at the occlusal surface. Labiolingual diameter is 13 mm at the occlusal surface. The tooth tapers towards the root, its basal diameters at the enamel junction are 8 mm transversely by 13 mm. This agrees with the incisors of the "Mpesida to Aterir" hipparion as shown by Hooijer (1987a). Mandibular i3 is unreduced unlike *Eurynathohippus*, its mesiodistal diameter is 13 mm and maximum labiolingual diameter is 10 mm at the occlusal surface.

EP 1341/01 is a left i1 (Fig. 12.19a, b). The tooth is long mesiodistally and both margins exhibit distinct, albeit light grooving.

LAET 75-1431 is a left p2 in middle wear. Figure 12.20a is a labial view showing a distinct, albeit slender ectostylid ascending the labial margin of the tooth. The ectostylid is not expressed on the occlusal surface (Fig. 12.20b) due to its relatively early stage of wear (crown height = 31.8 mm). The occlusal surface also exhibits a round metaconid, irregular kidney-shaped metastylid (not uncommon in early wear lower teeth), the linguaflexid is irregularly shaped, preflexid and postflexid have simple margins and the ectoflexid is deeply incised.

There is no p3 from the Upper Laetolil Beds. Figure 12.21 (a and b) are of a right p4, LAET 81-48 with a crown height of 49.6 mm. The labial view (Fig. 12.21a) reveals the straight mesial and distal walls typical of a p4 and a distinct ectostylid that is mesiodistally long at the base and tapers to a shorter length as the feature ascends the labial side of the crown. Figure 12.21b is of the occlusal surface, which includes a kidney-shaped metaconid, distolingually pointed

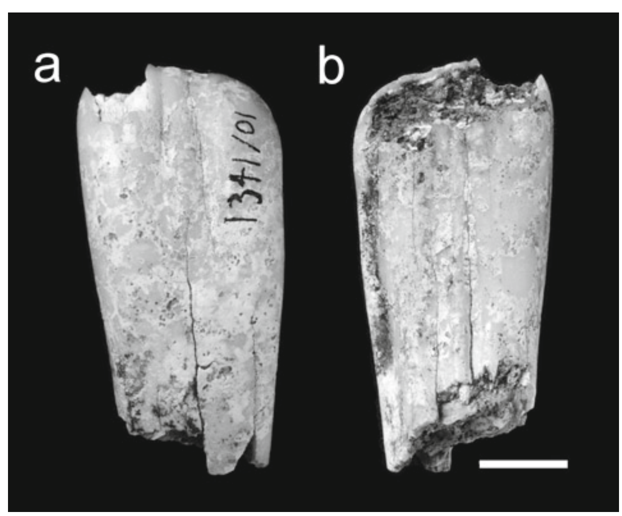

Fig. 12.19 (**a**) EP 1341/01, lt i1 (*labial* view). (**b**) EP 1341/01, lt i1 (*lingual* view). Scale = 1 cm

Fig. 12.20 (**a**) LAET 75-1431, lt p2 (*labial* view). (**b**) LAET 75-1431, lt p2 (*occlusal* view). Scale = 1 cm

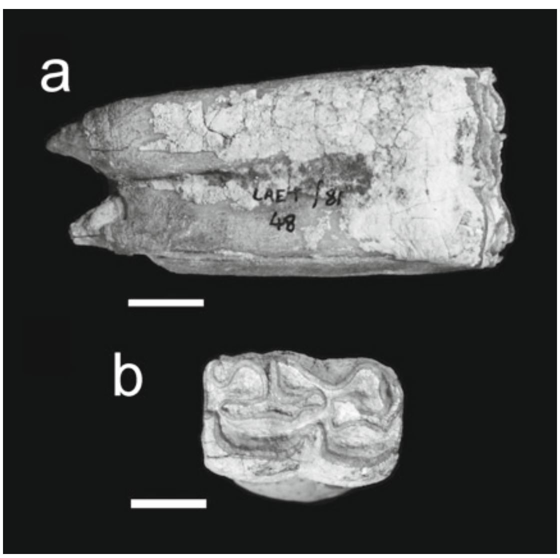

Fig. 12.21 (**a**) LAET 81-48, rt p4 (*labial* view). (**b**) LAET 81-48, rt p4 (*occlusal* view). Scale = 1 cm

metastylid, shallow linguaflexid, preflexid and postflexid with simple margins, ectoflexid deep with a distinct pli caballinid and the ectostylid is not expressed at the occlusal surface.

EP 1242/01 (Fig. 12.22) is a left m3 with a crown height of 68.6 mm. The labial view (Fig. 12.22a) shows the strong curvature of the mesial and distal margins typical of an m3. There is no evidence of an ectostylid in this view. The occlusal surface is worn enough to reveal a kidney-shaped

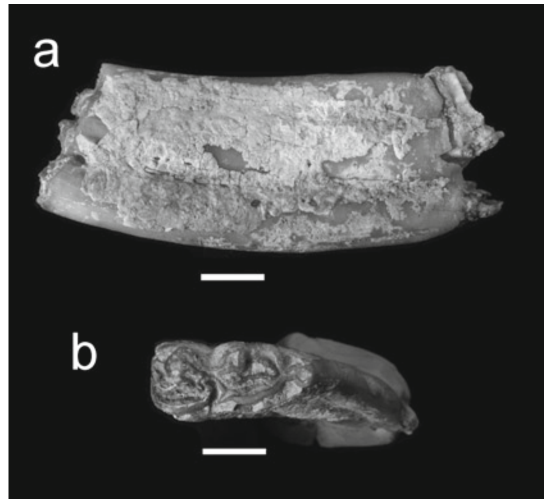

Fig. 12.22 (**a**) EP 1242/01, lt m3 (*labial* view), (**b**) EP 1242/01, lt m3 (*occlusal* view). Scale = 1 cm

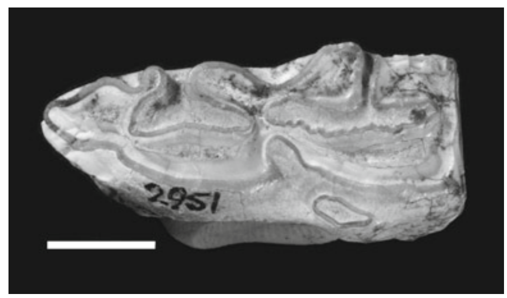

Fig. 12.23 LAET 75-2951, lt dp2 (*occlusal* view). Scale = 1 cm

metaconid and square shaped metastylid; linguaflexid is a deep and broad U-shape; preflexid has simple margins and postflexid has slightly complex margins; pli caballinid is distinct; ectoflexid is deep; hypoconulid has a double loop (Fig. 12.22b).

Upper Ndolanya Beds

LAET 75-2951 is a left dp2 (Fig. 12.23). The crown is short (9.2 mm high) and elongate and preserves the following salient features: metaconid is elongate and metastylid is square-shaped, linguaflexid is a deep, narrow U-shape, preflexid has simple margins whereas postflexid has a finely serrated margin, ectoflexid is shallow and a large oval structure.

LAET 74-253 from Loc. 18 is a mandibular symphysis that bears a canine described by Hooijer (1987a).

LAET 78-4815 is a left mandibular fragment with i1 and p3-m3, the dentition is much worn. Height of incisor crown from occlusal surface to enamel root border is 20.9 mm, width at enamel root junction is 10 mm and labiolingual

Fig. 12.24 (**a**) LAET 78-4815, lt mandible (*labial* view). (**b**) LAET 78-4815, lt mandible (*occlusal* view). Scale = 1 cm

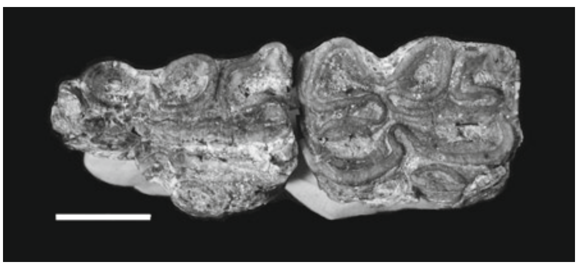

Fig. 12.25 LAET 75-3765, lt p2, p3 (*occlusal* view). Scale = 1 cm

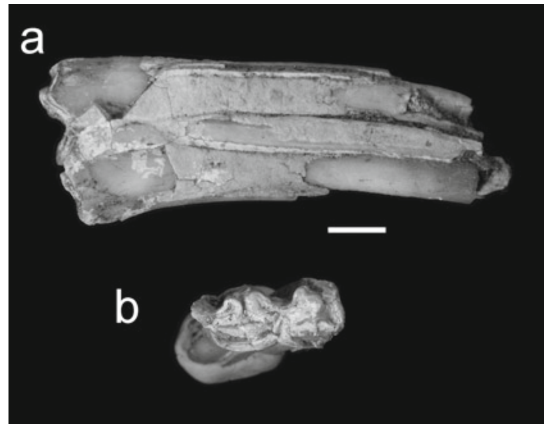

Fig. 12.26 (**a**) EP 1211/03, m2 (*labial* view). (**b**) EP 1211/03, m2 (*occlusal* view). Scale = 1 cm

diameter is 14.6 at this point. The labial view (Fig. 12.24a) includes only a little bone that covers p3-m3. Crown height is low on the m1 (33.8), m2 (39.1) and m3 (32.2) due to the advanced age of the specimen. The crown morphologies exhibit deep V-shaped linguaflexids on p3 and p4, deep and broader U-shapes on m1-m3; pre- and postflexids are labio-lingually compressed on p3 and p4, not so compressed on the molars; ectostylids present at the occlusal surface of p2-m3 and are very large on all cheek teeth, pli caballinids are not developed on any teeth and ectoflexid is deep only on the m3 and the m3 has a double hypoconulid. The metaconid and metastylid are somewhat angular, especially the metastylid. Length of tooth row is 158 mm.

LAET 75-3765 is a much worn p2 and p3 (Fig. 12.25). The p2s mesial and mesolabial margins is markedly eroded, however what is significant here is the compressed pre- and postflexids, shallow U-shaped linguaflexid and very prominent, large, oval ectostylid. The p3 is better preserved and has a very deep U-shaped linguaflexid; pre- and postflexids lacking any complexity, no pli caballinid and a very large ectostylid.

LAET 75-1685 is a left m1 with an ectostylid, which extends up to the occlusal surface. The height of the ectostylid as preserved is 60 mm. There is a protostylid. This is an important specimen because it is one of the few examples of a lower tooth associated with an upper dentition in this taxon.

EP 1211/03 is an early wear m2 with a crown height of 75.1 mm. Figure 12.26a exhibits the very large ectostylid on the labial wall of the tooth. The occlusal view (Fig. 12.26b) reveals that the tooth was in wear and must have been about 80 mm high preserving the following salient features: metaconid irregular shaped and metastylid pointed distally; pre and postflexid is compressed; linguaflexid is a broad U-shape; ectoflexid is deep; pli caballinid is lacking and ectostylid is not expressed on the occlusal surface.

We compare here the Upper Ndolanya Beds mandibular cheek teeth with the following Ethiopian mandibles (Fig. 12.27): Hadar AL 425-1 *Eurygnathohippus hasumense* mandible (Fig. 12.27a, Denen Dora 2, 3.2 Ma); Hadar AL 177-21, paratype of *Eurygnathohippus "afarense"* (Eisenmann 1977; Bernor and Armour-Chelu 1997; Bernor et al., 2010), mandibular symphysis (Fig. 12.27b, Denen Dora 2, 3.2 Ma); the Middle Awash BOU-VP-8-45 mandible (Fig. 12.27c) from the 2.5 Ma horizon (T.D. White, personal communication).

The AL 425-1 right mandible exhibits a number of characteristics common for *Eurygnathohippus hasumense*, and the Upper Laetolil Beds hipparions, metaconid is mostly rounded while metastylid is pointed posteriorly, premolar and m1 linguaflexids are a deep V-shape, while m2 is a deep U-shape. The AL 425-1 mandible is of an early adult stage-of-wear and the ectostylids are not well developed, nor is the i3 (only remaining incisor) fully erupted and in wear. The lack of ectostylid development in this specimen is due to its age, only, in that the ectostylid does not ascend to occlusal level in young adults. The cheek teeth do have the characteristic strongly developed pli caballinid typical of *Eu. hasumense.* AL 177-21 was referred to *Eurygnathohippus afarense* by Eisenmann (1977) based on its large incisors, but this was questioned by Bernor and Armour-Chelu (1997) and Bernor et al. (2010). Recently, Eisenmann and Geraads (2007) suggested that this specimen be reassigned to *Eurygnathohippus hasumense*.

Fig. 12.27 (**a**) AL 425-1 *Eu. hasumense* mandible from Denen Dora. (**b**) AL 177-2 *Eu. afarense* mandible paratype (Eisenmann 1977). (**c**) BOU-VP-8-45 mandible, Middle Awash. Scale = 5 cm

It may, in fact be referable to that taxon. What is important here is the large size of the erupted left i1-i2 and right i2. Mandibular i3 is in eruption, but would not have been very large when at full height. The symphysis is not mesiodistally strongly expanded as seen in *Eurygnathohippus cornelianus*. Hadar *Eurygnathohippus hasumense* mandibular tooth morphology compares well with the Upper Laetolil Beds cheek teeth and has a comparable maximum crown height of around 70 mm (Bernor et al., 2010). It also compares well with Upper Ndolanya Beds worn adult mandible LAET 78-4815 (see Fig. 12.24b).

The Middle Awash BOU-VP-8-45 mandible (Fig. 12.27c, 2.5 Ma) is slightly younger than the Upper Ndolanya Beds hipparion and is advanced in its morphology. It would appear to be of a young adult individual. The mandible is very deep, indicating advanced high crown height. The p3-m2 have elongate and narrow occlusal outlines, very broad and deep U-shaped linguaflexids, metaconids and metastylids that are sharply pointed lingualward and large (albeit broken) ectostylids. Upper Ndolanya Beds mandible fragment LAET 75-3765 (see Fig. 12.25), has large ectostylids on the p2 and p3, and a very deep linguaflexid on the p3. The Upper Ndolanya Beds EP 1211/03 right m2 exhibits the advanced characters seen in the BOU-VP-8-45 mandible, including: broad U-shaped linguaflexid, lingual pointing of the metaconid and metastylid and a large ectostylid.

Eisenmann and Geraads (2007) recently described a large, well-preserved sample of hipparion, *Eurygnathohippus pomeli* (*sensu* Bernor et al. 2010) from the 2.5 Ma Ahl al Oughlam fissure fills, Morocco. The mandibular material (Eisenmann and Geraads 2007, fig. 8) exhibits critical morphological features shared by the Upper Ndolanya and 2.5 Ma Middle Awash BOU specimens, most prominent being the large ectostylids, deep linguaflexids and propensity to have pointed metaconids and metastylids, particularly on the molar dentition. These features are likewise shared by the

Daka *Eurygnathohippus* cf. *cornelianus* from Ethiopia (Gilbert and Bernor 2008, figs. 6–19). We follow Bernor et al. (2010) in recognizing the increasing likelihood that these late Pliocene-Pleistocene taxa are closely related to one another.

Postcrania

We have described the size and proportions for astragali, calcanea, MC III, MT III and 1PH III in the statistical analysis. There is nothing further to add here for the astragali and calcanea because there are no discrete morphological characteristics by which they differ between stratigraphic levels at Laetoli and other Pliocene African hipparions that we have studied or have been reported by others. We do develop, albeit briefly below, some aspects of MP III and 1PH III morphology.

As noted earlier in the statistical summary we have no complete MC IIIs from Laetoli. The plots of proximal MC III width (M5) versus depth (M6) revealed an overlap in the Upper Laetolil and Upper Ndolanya Bed sample, but with most Upper Ndolanya specimens being smaller than the Upper Laetolil sample. Moreover, the Upper Ndolanya specimens are similar in size to the Höwenegg, Langebaanweg, and Manonga Valley specimen and some Olduvai specimens. The Upper Laetolil specimens overlap with the smaller specimens from Hadar. Figure 12.28 includes two specimens from the Upper Laetolil Beds (Fig. 12.28a, LAET 75-3138; Fig. 12.28b, LAET 75-2250) and the Upper Ndolanya Beds (Fig. 12.28c, EP 026/00; Fig. 12.28d, EP 927/00). All four specimens are similar in the extensive development of the magnum–hamate facet indicating well developed functional tridactyly. The two specimens from the Upper Ndolanya Beds do have a broader caudal articular surface than the two from the Upper Laetolil Beds. Whether this is a consistent and species-level difference has yet to be determined.

There is a single complete MT III from Laetoli, LAET 75-2471 from the Upper Ndolanya beds (Fig. 12.29a, b), and we compare it here to a Hadar MT III from the AL 155 skeleton collected from Denen Dora 2 (3.2 Ma; AL 155-6AZ, Fig. 12.29c, d). The bivariate plot comparisons (see Fig. 12.5a) and log 10 ratio comparisons (see Fig. 12.6b) clearly reveal that the Hadar specimen is much longer and the mid-shaft dimension is greater in the Hadar specimen than the Upper Ndolanya Bed specimen, but their basic proportions are otherwise very similar. Both the Laetoli and Hadar MT IIIs have prominently developed distal sagittal keels and distal epicondylar eminences, suggesting an adaption for open country running (Bernor et al. 2005). Interestingly, the MT III mean measurement of the Moroccan 2.5 Ma *Eurygnathohippus pomeli* (AaO) has an overall shape and proportion closer to the Upper Ndolanya Beds MT III than the Hadar hipparion (see Fig. 12.6b), and in turn, the Upper Ndolanya MT III compares closely with both the Daka (BOU-VP-13) and Olduvai *Eurygnathohippus cornelianus* mean measurements. These results suggest that the Upper Ndolanya Beds hipparion, the Moroccan mid-Pliocene hipparion and *Eurygnathohippus cornelianus* are potentially related and distinct from the *Eurygnathohippus hasumense* lineage.

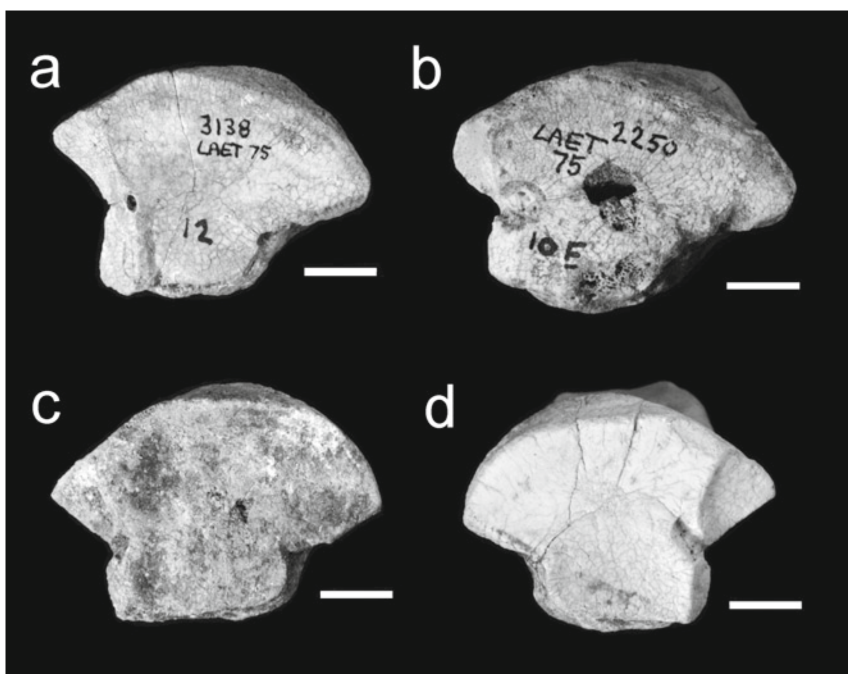

Fig. 12.28 (**a**) LAET 75-3138, proximal MCIII showing magnum-hamate facet from Upper Laetolil Beds. (**b**) LAET 75-2250, proximal MCIII showing magnum-hamate facet from Upper Laetolil Beds. (**c**) EP 026/00, proximal MCIII showing magnum-hamate facet from Upper Ndolanya Beds. (**d**) EP 927/00, proximal MCIII showing magnum-hamate facet from Upper Ndolanya Beds. Scale = 1 cm

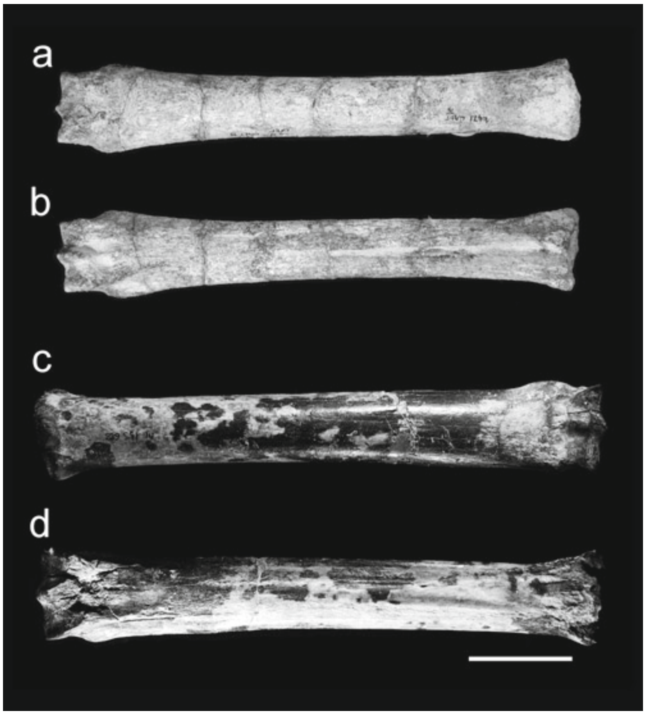

Fig. 12.29 (**a**) LAET 75-2471 MTIII (*anterior* view). (**b**) LAET 75-2471 MTIII (*posterior* view). (**c**) AL 155 MTIII (*anterior* view) Denen Dora. (**d**) AL 155 MTIII (*posterior* view) Denen Dora. Sacle = 5 cm

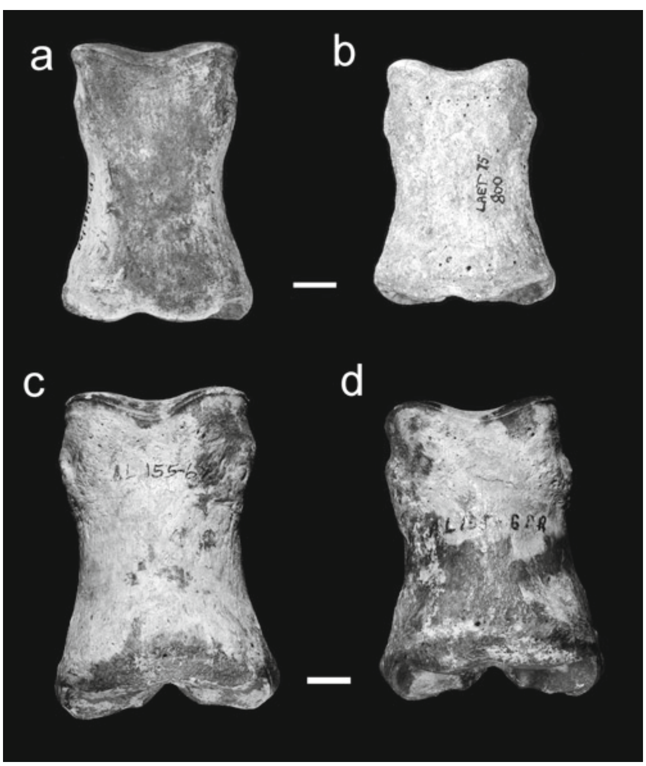

Fig. 12.30 (**a**) EP 3281/01, 1PHIII, Upper Laetolil Beds. (**b**) LAET 75-800 1PHIII, Upper Ndolanya Beds. (**c**) AL 155-6 X 1PHIII fore, Hadar. (**d**) AL 155-6 AA 1PHIII hind, Hadar. Scale = 1 cm

1PH III – Cranial and Caudal Comparisons

1PH IIIs reveal a similar pattern to the metapodials. Figure 12.30 includes four 1PH IIIs: EP 3281/01 (Fig. 12.30a, Upper Laetolil Beds), LAET 75-800 from 7E (Fig. 12.30b, Upper Ndolanya Beds) and AL 155-6 (6-AA is Fig. 12.30c and 6X is Fig. 12.30d). All four of these have the same basic morphology although they are of variable length. Figures 12.7a, b reveal that both the Upper Laetolil and Upper Ndolanya specimens are consistently smaller than those from Hadar. The log10 ratios diagrams show that the Hadar hipparion is longer than the Laetoli *Eurygnathohippus* mean, Langebaanweg and the Daka specimen (BOU-VP -12/89). An interesting point is that the AL 155 fore and hind phalanges show variation in length with AL 155-6AA being distinctly shorter (hind) than AL 155-6X (fore). The same proportional differences are found between the Upper Laetolil specimen (Fig. 12.30a) and Upper Ndolanya specimen (Fig. 12.30b). Finally, the bivariate plot of Laetoli 1PH III maximum length (M1) versus proximal articular width (M4, Fig. 12.7b) reveals that five Upper Ndolanya specimens lie in the middle of the Höwenegg ellipse, while one is distinctly above the ellipse, being somewhat longer. It is possible that these advanced Pliocene African hipparions are exhibiting differences in anterior versus posterior length as in extant *Equus*. Too little data exists to support this contention at this time.

Later Material

Equus from Emboremony 1 and 2 (Ngaloba Beds)

A few postcranial bones from Emboremony 1 and Emboremony 2 (Ngaloba Beds), dating to about 200 ka, can be referred to *Equus* sp. First phalanges EP 367/99, EP 2105/03, EP 351/99 are at the lower end of the range for *E. oldowayensis* and also overlap in size with *E. burchellii* (M1 greatest length 76–78 mm).

Systematics

EQUIDAE Gray, 1821
Eurygnathohippus van Hoepen, 1930

Generic Diagnosis: All African hipparions of the genus *Eurygnathohippus* are united by the synapomorphy of ectostylids on the permanent cheek teeth. Eurasian and North

American hipparions do not have this character, except rarely in extremely worn hipparion teeth from the Dinotheriensandes. Within *Eurygnathohippus* species crown height increases and ectostylid length, width and maximum height increase from older to younger stratigraphic horizons.

Eurygnathohippus cornelianus van Hoepen, 1930
The type specimen of *Eurygnathohippus cornelianus,* (COR 556), consists of a mandibular symphysis and associated lower incisors from Cornelia, South Africa, (van Hoepen 1930), and dated to around 900 ka. The type represents one of the latest specimens known of this taxon and may show some morphological advances over the earlier representatives from East Africa. The holotype of *Eu. cornelianus* is essentially defined by a set of lower incisors without any associated lower cheek teeth or upper dentition. Further material from the type locality described as *Eu. steytleri* may derive from the same taxon (Hooijer 1975).

Eurygnathohippus hasumense Eisenmann, 1983
Hipparion hasumense was first described from a lower tooth row (KNM-ER 2776) from Area 204 below the Hasuma Tuff in zones B and C of the Kubi Algi Formation (Eisenmann 1983). The Hasuma Tuff has a K–Ar date of 2.82 Ma, and is thus correlated with the early part of Member C of the Shungura Formation. It is also identified from zone A of the Kubi Algi Formation and the *Notochoerus scotti* zone, which lies below the KBS Tuff at Koobi Fora. Cranial remains from Hadar originally assigned to *Hipparion* sp. (AL 340-8, AL 116-115) are now also referred to this taxon (Eisenmann and Geraads 2007). AL 177-21 from the Denen Dora member, Hadar is the type specimen for *H. afarense*, and now referred to *Eu. hasumense* (Bernor and Armour-Chelu 1999; Eisenmann and Geraads 2007).

Eurygnathohippus hasumense is a large bodied taxon, especially individuals from the Hadar Formation, where its maximum size is documented. Individuals from the Turkana area, Laetoli and Manonga Valley are 10% smaller in postcranial dimensions, but larger than average upper cheek teeth from Laetoli are known from Locs. 1, 2, 9 and 12E (between Tuffs 5 and 8).

The muzzle is long and narrow (Eisenmann and Geraads 2007). Eisenmann (1983) found that the third and fourth lower premolars are notably larger than the first and second molars in this taxon. In Eisenmann's type specimen the cheek teeth are rather narrower than found in the Omo B11 (L1-40) mandible or Laetoli specimens, but are otherwise similar. In the material from Koobi Fora the lower cheek teeth usually possess ectostylids, which taper apically and are more visible in worn teeth. Forsten (1996) observed that the teeth from the lower Koobi Fora Formation resemble the large teeth from Vogel River, which lack or have small ectostylids and teeth from Members B and C of Shungura Formation identified as *Hipparion* sp.

VO MB 9/10 38 is a mandibular symphysis with the first incisors from Vogel River (synonymous with the Garusi River) attributed by Dietrich (1942) to *Hypsohipparion albertense*. The third incisors are missing, but were originally present and it is not *Eurynathophippus cornelianus* (Dietrich 1942, Plate 16).

Eurygnathohippus aff. *hasumense*
Upper Laetolil Beds. Differs from Hadar in relatively smaller size, less robust MP IIIs and 1PH IIIs than Hadar, smaller, less well-developed incisors, not as hypertrophied and lacking as strong labial and lingual grooving. The upper incisor arcade is more rounded and incisors of more equal mesiodistal length compared to *Eu. cornelianus*. Similar to Hadar hipparion in skull and cheek tooth morphology. Lower premolars larger than molars, as reported by Eisenmann (1983) for the type material of *Eu. hasumense*, and like Hadar in not having as well developed ectostylids, which are variably present in the Laetoli population. Pli caballinid (called the ptychostylid by Hooijer) is present in lower cheek teeth (Hooijer 1987a). Metaconid and metastylid somewhat angular. This species is similar to Moroccan *Eu. pomeli* in its MTIII proportions.

Eurygnathohippus aff. *cornelianus*
The Laetoli sample of *Eu.* aff. *cornelianus* is similar in cheek tooth crown height and MC III, MT III and 1PH III dimensions to *Eu.* aff. *cornelianus* from Daka and in postcranial proportions to *Eu. cornelianus* from Olduvai. Crown height in Olduvai Bed IV hipparions approaches 90 mm, whereas in Bed II, as well as in the Upper Ndolanya Beds they are approximately 80 mm. The length of the lower cheek tooth row is 158 mm in LAET 78-4815, (Loc. 18), and similar or slightly shorter than found in *Eu*. *hasumense* (161 mm) in AL 177-21 (Eisenmann 1976) and 169 mm in LAET 74-491 from Loc. 11, Laetoli. The length of the premolar row is around 75 mm and approximately of subequal length with the molar row. Eisenmann (1983) notes that the premolars are relatively small. Metaconids and metastylids often have a rounded morphology and the longitudinal enamel crests of the preflexid and postflexid are often rather straight, described as the "caballoid" condition (Forsten 1996).

Discussion

One of the points of difference between *Eu. hasumense, Eu. turkanense, Eu*. aff. *hasumense* and *Eu*. *cornelianus* is the degree of hypsodonty of the incisor teeth (Hooijer 1975), although mesiodistal dimensions of the occlusal surface of lower first and second incisors are similar. We do not have measurements for unworn upper incisor teeth of *Eu.* aff. *hasumense.* However, LAET 75-3473, I1 has a mesiodistal length of 18 mm and a height of 25 mm (Hooijer 1987a).

Hooijer (1987a) notes the similarity between this incisor and those found in the type skull of *Eu. turkanense* and the same dimensions in the I2 of the WM 1528/92 skull are 18 mm at a height of 39 mm.

Hooijer (1975) reports a maximum height of 80 mm in a relatively unworn first upper incisor BK II, 264 of *Eu. cornelianus* (measured along the curvature of the tooth). The mesiodistal length is unknown in this specimen, but in the associated I2 it is 22 mm.

The Olduvai series described by Hooijer (1975) gives the range of dimensions of the occlusal surfaces of the incisor teeth from early to late wear stages. Mesiodistal dimensions of upper first and second incisors ranges between 17 and 22 mm (Hooijer 1975), whilst the maximum mesiodistal length of *Eu. hasumense* I2s is 18 mm.

The morphology of incisors attributed to *Eu. hasumense* also differs from the condition found in *Eu. cornelianus*. In *Eu. hasumense* the crown of the incisors tapers to the tooth root, whereas in *Eu. cornelianus* they are relatively broader at the cementum–enamel border. *Eurygnathohippus cornelianus* typically has broad ridge along the labial surface of the upper first incisor, but this feature is also found in some *Eu. hasumense* material.

The height of the i2 in *Eu. hasumense* (AL 155-6), a young adult, is 49 mm (Eisenmann 1976). The mesiodistal dimensions of the first and second lower incisors of *Eu. hasumense* (AL 177-21), which is also a young adult are 18 mm for i1 and 23.5 for i2 (Eisenmann 1976), similar to the mesiodistal length of 21 mm in the i2 from Manonga Valley (WM 1470/92), compared with 21 mm in an unworn i1 of *Eu. cornelianus* from Olduvai, (SHK II, 749).

Dimensions of the Upper Ndolanya lower incisors appear slightly smaller than the material described by Hooijer (1975) from Bed II, Olduvai, but the Laetoli sample are largely derived from old animals where the crown height does not exceed 25 mm.

The sequence of hipparion remains from Laetoli is important in that it documents the replacement of *Eu.* aff. *hasumense* with fairly hypsodont cheek teeth and variably present ectostylids, (usually more evident in the later tooth wear stages), by an early member of the *Eu.* aff. *cornelianus* lineage. The cheek teeth of *Eu.* aff. *cornelianus* are more hypsodont although slightly smaller than *Eu.* aff. *hasumense* and have well developed ectostylids which are consistently present throughout the population.

The earliest occurrence of *Eu.* aff. *cornelianus* appears to be the Upper Ndolanya Beds at Laetoli, which is interesting in the regard that this immediately postdates an intense climatic drying phase at around 2.8 Ma. During the 2–1 million year interval the taxon is widely represented throughout East Africa, (Daka and the Omo Valley, Ethiopia; Olorgesaillie, Kenya; and Olduvai Gorge, Tanzania). Its last reasonably well calibrated occurrence is in eastern Africa at 900 ka and at Olduvai, Bed IV. There may be later occurrences in South Africa (for type site Uitsoek, Cornelia dated between 1.0 and 0.6 Ma), but these are not well calibrated (Bernor et al. 2010).

Despite some similarities between *Eu. cornelianus* and *Eu. hasumense* such as grooving on incisor teeth, some reduction in the size of the lower third incisor, relatively hypsodont cheek teeth, *Eu. cornelianus* is not likely descended from *Eu. hasumense*. In *Eu. hasumense* the proportions of the postcrania are dissimilar to *Eu. cornelianus* and are more derived. The proportions of limbs may suggest a closer affinity to *Eu. hooijeri* from Laangebaanweg (Bernor and Kaiser 2006), which also shows advances in the degree of hypsodonty and ectostylid development.

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