Systematics and Paleobiology of \emph{Hippotherium malpassii} n. sp. (Equidae, Mammalia) from the latest Miocene of Baccinello V3 (Tuscany, Italy)

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ABSTRACT - A new species of hipparionine horse, \emph{Hippotherium malpassii}, is described from the MN13 interval from localities of the Baccinello V3 area (Italy). This species exhibits some advanced features of the facial region and cheek tooth dentition while other skull features and the postcranial skeleton are plesiomorphic. Research related to paleodiet suggests that \emph{Hippotherium malpassii} was a mixed feeder, not as committed to grass feeding as many Central European species of \emph{Hippotherium}. However, it may be considered as being similar to others such as \emph{Hippotherium primigenium} from Eppelsheim (Germany) and \emph{Hippotherium} microdon from Baltavar (Hungary). Studies of carbon and oxygen isotopes suggest that \emph{Hippotherium malpassii} from the Baccinello V3 area lived in a forested context and it is inferred herein that it likely ate grass of relatively low abrasive character. Regarding the paleogeography of the species, \emph{Hippotherium} originated in Central Europe early on in the MN9 interval (ca. 11 Ma) and underwent a modest evolutionary radiation there during the Vallesian and early Turolian (MN9-11). It is documented as having then dispersed throughout the Balkans into Greece during MN11/12 where it is represented by \emph{Hippotherium} brachypus from the locality of Pikermi (Greece). During the interval MN12, the range of \emph{Hippotherium} brachypus was extended and populations of very large size with massive metapodials evolved throughout this period. \emph{Hippotherium} is not documented from the Baccinello area in Tuscany until the base of the MN13 interval (Baccinello V3 faunas) and may have immigrated from the Pannonian Basin, Hungary. The genus \emph{Hippotherium} would appear to have become extinct at the end of MN12, the latter considered as being a result of increased continental drying and reduction of forest and woodland habitat. Its occurrence at Baccinello V3 in the MN 13 interval represents the latest occurrence of the genus in Europe.

KEY WORDS - \emph{Hippotherium} malpassii n. sp., Systematics, Paleoecology, Baccinello-Cinigiano Basin, V3 fauna, Late Miocene, Messinian, Tuscany, Italy.

INTRODUCTION

The geology and paleontology of the Baccinello area are well known thanks to the early research led by Johannes Hürzeler (1908-1995) from the Basel Naturhistorisches Museum which recovered abundant faunal remains from well documented stratigraphic levels (De Terra, 1956; Lorenz, 1968; Hürzeler & Engesser, 1976). Since the late 1990s, research undertaken by the Vertebrate Paleontology Research Group of the University of Florence (after the initial contributions of the late Claudio De Giuli, 1938-1998) has increased our knowledge of paleontology, geology and sedimentology of the area (Benvenuti et al., 1994, 1999, 2001; Rook et
al., 2000, 2006, 2011; Ligios et al., 2008), providing a better understanding of the sedimentary, environmental and faunal evolution of the Baccinello-Cinigiano Basin (thereafter referred to as BCB).

The Baccinello hipparion samples in the Basel Naturhistorisches Museum (NHMB) and Museo di Storia Naturale (Sezione Geologia e Paleontologia) of the University of Florence (IGF), include a complex series of fossil localities distributed over 100 square kilometers (Figs 1-2). Specimens usually outcrop as either individual, or as handful of specimens from small, discrete localities. Moreover, the Late Miocene is a time when there were multiple lineages of hipparion known from Central Europe and the peri-Mediterranean realm, the most species diverse lineages being *Hippotherium*, *Cremohipparion* and *Hipparion s.s.* It would not at all be unexpected to discover multiple species of hipparion from the Baccinello V3 localities. This study challenges us to assemble hypodigms in a clear and logical manner.

Since the Baccinello V3 equid fauna is so distinct, we will further undertake a paleodietary study using the mesowear method of Fortelius & Solounias (2000). We also include a study of habitat reconstruction as expressed by carbon and oxygen isotope studies of the type specimen of *Hippotherium* malpassii n. sp. from Baccinello V3. We follow Bernor et al. (1997) in interpreting the functional anatomy of *H. malpassii*. This study establishes that *Hippotherium malpassii* has a biogeographic history connected to Central Europe.

Other, smaller, rarer and more poorly represented Baccinello V3 equids may have an apparent evolutionary relationship to eastern and southern Mediterranean forms of the genus *Cremohipparion*. Their description is beyond the scope of this paper.

**GEOLOGICAL CONTEXT**

The BCB is a Late Neogene basin located 25 km east of Grosseto in southern Tuscany (Figs 1-2), being one of the largest Tuscan “central basins”, (sensu Martini & Sagri, 1993). The BCB records a continental sedimentation throughout the late Tortonian-Messinian. The basin (Fig. 2) is filled with a minimum of 250 m of Late Miocene continental conglomerates, sands, silty clays bearing lignite seams, and freshwater carbonates (Lorenz, 1968; Benvenuti et al., 1999a, b, 2001).

Before the middle of the last century, only scattered areas of the BCB were the object of concerted research, and these investigations were mainly related to lignite exploitation (e.g. Stoppani, 1880). The first stratigraphic investigations in the Basin began in the late 1950s (De Terra, 1956; Lorenz, 1968). Lorenz (1968) described the complex lithostratigraphy, which included the occurrence of numerous vertebrate-bearing fossiliferous levels. In recent times this Late Miocene succession has been referred to two unconformity-bounded stratigraphic units (synthems 1-2, Benvenuti et al., 2001; Fig. 2). Synthem 1 (late Tortonian-early Messinian) unconformably resting on the pre-Tortonian substratum made of limestone, claystone and sandstone is further subdivided into six main units, in some cases with sub-units, deposited within different paleoenvironments, ranging from slope-palustrine settings to peat bogs to shallow lakes, alluvial plains and deltaic-lacustrine settings (Benvenuti et al., 2001). Fine grained deposits in the different units bear relatively abundant fossil mammal remains that are grouped into distinct assemblages (vertebrate assemblages V0, V1, V2, and V3; Lorenz, 1968; Engesser, 1983, 1989; Rook & Rustioni, 1991; Rook et al., 1991, 1996,
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1999, 2000, 2008; Rook & Torre, 1995; Rook, 1999, 2009; Abbazzi, 2001; Bernor et al., 2001; Eronen & Rook, 2004; Abbazzi et al., 2008; Rook & Martinez Navarro, 2004; Chesi et al., 2009; Angelone & Rook, 2011; Casanovas-Vilar et al., 2011a, b; Gallai & Rook, 2011. Mollusc-rich levels characterize specific lacustrine mudstone and limestone, known in literature as F1 and F2 (Gillet et al., 1965; Esu & Girotti, 1989; Ligiós et al., 2008). Synthem 2 (late Messinian) rests unconformably on the deposits of Synthem 1 and is referred to the late Messinian, since Early Pliocene marine deposits ascribed to the *Sphaeroidinellopsis* Zone stratigraphically overlies it (Bossio et al., 1991; Benvenuti et al., 2001).

Rook et al. (2011), provided a synthesis of the BCB geological setting and support the chronological range of the depositional history of the sedimentary succession based on a well resolved magnetostratigraphic section. The Baccinello V3 fauna is magnetostratigraphically correlated to Chron C3An, early Messinian, ca. 6.733 to 6.436, and MN13 (Fig. 3).

**Hippotherium localities**

The sedimentary unit yielding the V3 faunal assemblage (Unit 1e, as defined by Benvenuti et al., 2001) is the one within the BCB sedimentary succession that widely outcrops across the basin’s geographical extension (Figs 1-2). The gaiacite setting of the geological units together with the geomorphic characteristics of the area and the erosion patterns versus human use of the region has the combined effect to concentrate the V3-fossil bearing
Fig. 3 - Stratigraphic columns magnetostratigraphically calibrated for reference sections in the southern (La Locca) and north-western (Ribaldella) sectors of the BCB respectively (cfr. Fig. 1). The type locality for *Hippotherium malpassii* (Podere Firenze) is litostratigraphically correlated with Ribaldella section (modified after Rook et al., 2011).
outcrops on the north-western and southern portion of the Basin, on the right banks of the Trasubbie river (to the south) and the Melacce river (to north-west). Most of the recent single-specimen collections are recorded in museum catalogues as single spot localities, while specimens gathered from the earliest field work provide only a general indication of local jurisdictions provenance. In terms of local jurisdictions, the BCB areas falls just on the junction of 5 different municipalities which cause us to subdivide the BCB into five different sectors (Fig. 1): Cinigiano, the north and western portion up to the Melacce river; Arcidosso, the eastern central portion, east of Melacce river and north of Melacchio stream; Roccabelgna, the southeastern portion, south of Melacchio stream, including the upstream portion of the Trasubbie valley; Scansano, the southwestern portion, the downstream portion of the Trasubbie valley (includes the hamlet of Baccinello); Campagnatico, the western central portion.

METHODS

We will compare the Baccinello V3 hipparions to a relevant group of Late Miocene Old World hipparions that we refer to the Hippotherium lineage (Tab. 1). These include Central European Vallesian Hippotherium from the German localities of Höwenegg (indicated by a “h” on the ensuing bivariate plots) and Eppelsheim (e on the plots). Also included are the Austrian Vallesian localities of Inzersdorf (i) and Gaiselberg (g), the Hungarian Vallesian locality of Rudabánya (r) and Turolian age localities of Baltavar (t) and Polgardi (o). We also include statistical comparisons to “Cormohipparion” sinapensis from the Turkish Vallesian localities of Esme Akacoy (y) and Sinap (s). Baccinello V3 is a late Turolian locality indicated in our plots as a “B”. These taxa and the age of their localities have been discussed in several previous studies (Bernor et al., 1988, 1993, 1996, 1997, 2003a, b; Kaiser et al., 2000, 2003; Bernor & Scott, 2003; Scott et al., 2005a, b; Woodburne, 2007).

We analyse here the following skeletal elements following previous studies cited above: maxillary P2, astragali (hereafter AST), calcanea (CALC), metacarpal III’s (MCIII’s), metatarsal III’s (MTIII’s; MCIII’s and MTIII’s collectively will be referred to as MPIII’s) and 1st phalanges III’s (1PHIII’s) using standard equal measurements published by Eisenmann et al. (1988) and Bernor et al. (1997). Measurements of the Baccinello V3 hipparions are provided in Appendix 1.

For cheek teeth we use the Eppelsheim sample as our standard for calculating 95% confidence ellipses (following Bernor & Franzen, 1997; Bernor et al., 2003b). The Eppelsheim sample is superior because it is a large sample of a primitive Old World hipparion composed almost entirely of isolated cheek teeth from a single quarry. This allows measurements at all stages of ontogeny. For postcranial elements we use the Höwenegg sample as our analytical standard for the postcranial skeleton. This population is composed of 16 articulated skeletons (many of which are complete), along with isolated bones and is “biologically uniform”, including only a single primitive species, Hippotherium primigenium Meyer, 1833 (Bernor et al., 1997). This sample has been found to be particularly useful for statistical comparisons of postcranial elements. Indeed, the possibilities for broad comparative study of hipparion metapodials are greatly expanded by the extraordinary preservation of, and body of scholarship on, hipparions from Höwenegg (Bernor et al., 1997; Scott, 2004).

Two statistical methods are used. In the first, we generate a series of bivariate plots which include 95% confidence ellipses using the Eppelsheim sample for cheek teeth and the Höwenegg sample for postcranial elements as prescribed above. These plots allow a visual representation of how Baccinello V3 compares to our comparative sample for some key morphological features. We also use log10 ratio diagrams strictly for our MCIII, MTIII and 1PHIII samples. Traditionally, log10 ratio diagrams have been used as a descriptive tool in discussions of hipparion morphology (e.g., Eisenmann, 1995). We apply this approach here to MPIII’s and 1PHIII’s. Log10 ratio diagrams graphically illustrate deviations from a comparative standard (in this study the Höwenegg population sample) and are a descriptive heuristic. Profiles shown in ratio diagrams represent absolute deviations from a morphometric standard.

For mesowear analysis we apply here the mesowear methodology originally formulated by Fortelius & Solounias (2000). Fortelius & Solounias (2000) and Kaiser et al. (2000) found that the mesowear signal allows a reasonable scoring of paleodietary preference when the sample size is 10 dental specimens or greater. A statistically stable paleodietary signal can be expected when the sample size is 10­30 individuals. The sample size available to this study is much too small to obtain a statistically sound mesowear classification if the standard methodology is followed. In order to gain a reasonably accurate scoring of our sample, we abandon conventional practice here as follows: 1) tooth positions other than upper M’s are included, 2) lower teeth are included. Scorings of mandibular teeth are calibrated following Kaiser & Fortelius (2003) for the Eppelsheim sample of Hippotherium primigenium.

Hierarchical cluster analysis with complete linkage (furthest neighbours) is applied here following the

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Tab. 1 - Late Miocene Old World hipparions comparative sample. Letters refer to locality designations used in bivariate plots of Figs 4-7, 9 and 11.
standard hierarchical amalgamation method of Hartigan (1975). The algorithm of Gravaeus & Weiner (1972) was then used to order the cluster tree using the three mesowear variables (% high, % sharp and % blunt). As a comparative dataset for dietary classification, we use 27 extant mammalian ungulate species reported as “typical” dietary categories by Fortelius & Solounias (2000). As comparative datasets for fossil hipparionine horses, we include mesowear signatures of four Old World Hipparion taxa, Hippotherium primigenium from the MN9 of Eppelsheim (Dinootheriensande, Germany; Kaiser, 2003), Hippotherium primigenium from MN9 of Höwenegg (Germany; Kaiser, 2003), Hippotherium aff. primigenium and Hippotherium kammerschmittae from MN11 of Dorn-Dürkheim (Germany; Kaiser et al., 2003), Hippotherium sumegense (Hungary; Bernor et al., 1999) and Hippotherium intrans (MN 9 of Rudabánya, Hungary; Bernor et al., 2003a). We further apply Principal Components Analysis (PCA) on mesowear parameters of each of the above mentioned datasets. As in the cluster analysis, we include 27 “typical” extant ungulate species after Fortelius & Solounias (2000) as comparative species with known diets. Systat 9.0 software was used to compute cluster statistics, using default settings.

For stable isotope analysis a tooth is sampled three times from crown to root. Samples of pure enamel were removed using a Dremel high-speed rotary tool with a diamond-impregnated bit. Samples were run using an automated carbonate microsample device. Each isotopic sample consisted of 0.5-0.7 mg of enamel, and samples were washed with 3% hydrogen peroxide for 15 minutes and rinsed, followed by 0.1M acetic acid for 15 minutes and rinsed. Samples were then reacted with 100% phosphoric acid at 90°C on the automated carbonate device interfaced with a Finnigan MAT 252 stable isotope ratio mass spectrometer. Isotopic ratios are presented in the per mil (%o) notation

\[ d^{13}C \text{ (or } ^{18}O) = \left( \frac{R_{\text{sample}}}{R_{\text{PDB}}} - 1 \right) \times 1000 \]

where \( R_{\text{sample}} \) and \( R_{\text{PDB}} \) are the ratios \(^{13}C/^12C\) (or \(^{18}O/^16O\)) in the sample and standard respectively, and the isotope reference standard is PDB. Oxygen values are reported assuming the acid-calcite fractionation factor for calcite.

Abbreviations and Conventions

Abbreviations - IGF: Museo di Storia Naturale (Sezione Geologia e Paleontologia), University of Florence; NHMB: Naturhistorisches Museum, Basel; AST: astragali; CALC: calcanea; MCHIII: metacarpal III; MTIII: metatarsal III; MPIII: metapodial III; 1PHIII: 1st phalanx III.

Measurements - Measurement numbers (M1, M2, M3, etc.) refer to those published by Eisenmann et al. (1988; and rounded to 0.1 mm) for the skulls and postcrania (also in Bernor et al., 1997), whereas tooth measurement numbers refer to those published by Bernor et al. (1997), Bernor & Franzen (1997) and Bernor & Harris (2003).

Anatomical Descriptions - 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.

Conventions - The nomen Hipparion has been used in a variety of ways by different authors. We follow characterizations and definitions for hipparionine horses recently provided in Bernor et al. (1996, 1997). Anatomical descriptions have been adapted from Nickell et al. (1986). Getty (1982) was also consulted for morphological identification and comparison. Hipparion monographs by
Gromova (1952) and Gabunia (1959) are cited after the French and English translations. The taxon *Hipparion* has been applied in a variety of ways by different authors. We utilize the following definitions in this work:


- **Hipparion s.s.** - the name is restricted to a specific lineage of hipparionine horses with the facial fossa positioned dorsally high on the face (MacFadden, 1980, 1984; Woodburne & Bernor, 1980; Woodburne et al., 1981; MacFadden & Woodburne, 1982; Bernor, 1985; Bernor & Hussain, 1985; Bernor et al., 1987, 1989; Woodburne, 1989). The posterior pocket becomes reduced and eventually lost, and confluent with the adjacent facial surface (includes Group 3 of Woodburne & 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*" and Old World *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* (Bernor et al., 1980; Woodburne & Bernor, 1980; MacFadden & Woodburne, 1982; Bernor, 1985; Bernor & Hussain, 1985; Bernor et al., 1987, 1989; Woodburne, 1989). We emphasize here the need to avoid confusion of well defined hipparionine lineages with poorly characterized taxa of "*Hipparion*" sensu lato.

- **Hippartherium** - a discrete genus of Western Eurasian hipparionine horses known from Central Europe, Italy, Greece and possibly Ukraine. Species belonging to this genus include *H. primigenium*, *H. intrans*, *H. microdon*, *H. kammerschmittei*, *H. malpassii* n. sp. (this contribution), *H. brachypus* and perhaps *H. giganteum*.

### STATISTICAL ANALYSES

Fig. 4 provides a bivariate plot of P₂ occlusal width (M3) versus occlusal length (M1) with a 95% confidence ellipse based on the Eppelsheim (Germany, MN9) sample. Fig. 4a includes a large sample of P₂'s. Most of our sample falls within the Eppelsheim ellipse, including: Rudabánya (r), Höwenegg (h), Gaiselberg (g), and a particularly large sample from Baltavar (t). The Baccinello V3 P₂'s (B) all fall in the center, lower right and (one) just outside the right margin of the ellipse. Baltavar is represented by several specimens, most in the lower portion or just outside the lower margin of the ellipse. Gaiselberg has two specimens in the lower portion of the ellipse and a single specimen well below the ellipse. Overall, the vast majority of specimens fall within the ellipse and the outliers outside the ellipse are not substantially smaller than Eppelsheim *Hippartherium primigenium*. Fig. 4b plots P₄ protocone width (M11) versus protocone length (M10) with no address to an Eppelsheim 95% ellipse. A general characteristic of the Baccinello V3 hipparions is that the protocone is short, giving it a rounded aspect. The Vallesian localities of Gaiselberg (g) and Höwenegg (h) have longer protocones than most of the Baccinello V3 sample. Baltavar (t) compares closely with Baccinello V3 falling in the middle of the Baccinello range. Baccinello V3 has a total width range (M11) of 3.3 to 5.6 and total length range (M10) of 4.2 to 7.2 which is less than that of Höwenegg: 3.1 to 6.6 and 5.8 to 8.8, respectively, and therefore not indicative of representing more than a single species in the Baccinello V3 sample. Bernor et al. (2003a) noted the small, rounded protocone present in a hipparion from the Hungarian MN 13 locality of Hatvan.

Fig. 5 is a bivariate plot of astragalus length (M1) versus distal articular width (M5), compared to the Höwenegg standard. The Baccinello V3 (B) astragali mostly fall within the lower half of the ellipse with a single specimen falling to the left of the ellipse. Eppelsheim (e), Rudabánya (r), Inzersdorf (i) and Gaiselberg (g) mostly fall in the lower portion of the ellipse also. Polgardi has most of its specimens plotting in the lower part, or just below the ellipse. Baltavar (t) is similar to Polgardi in this regard, but has several specimens that are even smaller. In the cases of Rudabánya, Baltavar and Polgardi, there is a smaller hipparion known from these localities (Scott...
et al., 2003), but in some of these the smaller size may be due to the juvenile status of the individual sampled; it is very difficult to ascertain juvenile status of astragali. The result of this analysis suggests that there is more than a single sized hipparion that exists in several of these locality samples.

Fig. 6 plots the known calcanea in our sample for maximum length (M1) versus maximum width (M6). Specimens plotted within the ellipse include Eppelsheim (e), Rudabánya (r) and Inzersdorf (i). Baccinello V3 (B) plots just outside the lower border of the ellipse and also far before the lower border; this latter, smaller specimen may be of a different species than H. malpassii n. sp. since a rare, smaller horse is already known from the cheek teeth. Rudabánya (r) includes two specimens, one on the lower border of the ellipse and one just outside the lower border of the ellipse. Baltavar (t) has an extremely small specimen very far below the ellipse that may represent a rare (other than Hippotherium intrans and Hippotherium microdon), third species in the fauna. The Sinap specimen (s) is referable to C. sinapensis (Bernor et al., 2003b) which has been shown to be smaller than Central European Vallesian Hippotherium primigenium.

Fig. 7a plots MCIII maximum length (M1) versus distal articular width (M11) compared to the Höwenegg standard 95% confidence ellipse. Most specimens fall within the Höwenegg ellipse, including 2 specimens from Baccinello V3 (B) in the middle of the ellipse, 4 specimens from Esme Acakoy (y), 4 specimens from Inzersdorf (i), 2 from Sinap (s; C. sinapensis), and 6 specimens from Baltavar (t) in the lowermost portion of the ellipse. One specimen from Inzersdorf (i) plots to the right of the ellipse, while 5 specimens from Baltavar (t) plot below the ellipse. Baltavar (t) Hippotherium microdon is once again shown to be a small member of the Hippotherium clade with several specimens falling in the lower portion of the ellipse, or below the ellipse. Most of the Pikermi specimens of Hippotherium brachypus plot within the Höwenegg ellipse, with one plotting to the right of the ellipse. Samos has two specimens plotting in the upper part of the ellipse and two well above the ellipse. These larger Samos specimens overlap with several specimens of Hippotherium “brachypus” from Akkasdagi, Turkey (Vlachou & Koufos, 2009). We believe that these larger specimens of Hippotherium “brachypus” from Samos and Akkasdagi are of an advanced member of the
Hippotherium brachypus clade. Fig. 7b plots MCIII distal midsagittal keel (M12) versus distal articular width (M11). The results are essentially the same as for Fig. 7a and we include this plot here to emphasize the consistently larger size of the advanced Hippotherium “brachypus” from Samos (x) and Akkasdagi (k).

Fig. 8 includes Log 10 ratio diagrams of MCIII. Fig. 8a compares the two Baccinello V3 MCIII’s to relevant Vallesian Hippotherium spp. from Inzersdorf, Austria (MN 9; Bernor et al., 1988), Cormohipparion sinapensis from Esme Acakoy, Turkey (MN 9; Bernor et al., 2003b), the Dinotheriensandes Hippotherium primigenium, and Rudabanya Hippotherium intrans compared to the Höwenegg mean Log 10 standard. The Vallesian MCIII sample is remarkably similar in its dimensions with Rudabanya Hippotherium intrans being the longest MCIII.
and Inzersdorf *Hippotherium primigenium* being the shortest MCIII. The remaining Vallesian *Hippotherium* samples are similar in length, most have relatively slender mid-shaft widths (M3) versus mid-shaft depths (M4) referred to as the “Esme Acakoy Effect” (Bernor et al., 2003b; Scott, 2004). Baccinello V3 specimens IGF 8192V and IGF 9397V (Plate 1, figs 1,2) show variability, but have very similar Log10 ratio profiles (except M6, proximal articular depth, with IGF 8192V being smaller) suggesting that they are of the same species and related to other members of the *Hippotherium* clade. Together they mostly bracket the rest of the sample in their morphology. Fig. 8b replots the Baccinello V3 MCIII’s compared to Turolian members of the *Hippotherium* clade. Once again, this plot exhibits the same proportional relationships of maximum length (M1), mid-shaft width (M3) and mid-shaft depth (M4) as found in the Vallesian taxa. Here, Baccinello’s Log 10 ratio would appear to track most closely with the Polgardi mean measurements while Baltavar (Kaiser & Bernor, 2007) and Dorn Dürkheim (Bernor & Franzen, 1997; Kaiser et al., 2003) compare particularly closely to one another except for the former’s shorter maximum length measurement (M1). As per the bivariate plots, Samos *Hippotherium “brachypus”* (here SAM_Hbra2) plots along with Akkasdagi *Hippotherium “brachypus”* with much larger dimensions than the rest of the sample. We distinguish further here a smaller form of Samos *Hippotherium “brachypus”* which has a MCIII that has a very short maximum length (M1) and is similar to Pikermi *Hippotherium brachypus* in not showing the Esme Acakoy effect: midshaft width (M3) is not proportionally narrower than M4. This smaller member of the *Hippotherium brachypus* clade (Hbra1 here) is known from Samos Quarry 6, while the larger form (Hbra2 here) is from Samos Quarry 1, 2 and 4.

Fig. 9a plots MTIII maximum length (M1) versus distal articular width (M11) compared to the Höwenegg standard 95% confidence ellipse. Again, most of our sample plots within the Höwenegg ellipse, including: 7 specimens from Esme Acakoy (y; C. sinapensis), 4 specimens from Inzersdorf (i), 1 from Gaiselberg (g) and 2 from Polgardi (o). There is one Baccinello V3 specimen that plots on the lower left border of the ellipse (B). Rudabánya (r) has a specimen that plots slightly above the ellipse while there are specimens from Esme Acakoy (y) and Sinap (s) that plot on the left side of the ellipse. While there are 3 Baltavar specimens (t) that plot within the ellipse, most of the Baltavar specimens, referable to *Hippotherium microdon* plot at the lower boundary or below the Höwenegg ellipse. Once again, all Pikermi specimens of *Hippotherium brachypus* plot within the upper half of the Höwenegg ellipse, except for one that plots just outside the right border of the ellipse. There is a single Samos specimen of *Hippotherium “brachypus”* (Hbra1) that plots in the center of the ellipse (x), while others plot at the top of the ellipse. There are two specimens of the larger Samos *Hippotherium “brachypus”* at the top and outside the upper border of the ellipse overlapping in their size with Akkasdagi *Hippotherium “brachypus”*. Fig. 9b plots MTIII distal midsagittal length (M12) versus distal articular width (M11). Interestingly, this plot shows that Pikermi *Hippotherium brachypus* shows a trend toward increased midsagittal length (M12) that is at the top and above the Höwenegg ellipse overlapping with Samos advanced, large *Hippotherium “brachypus”*. A specimen from Samos (x) is extremely large plotting well above all other specimens. Another specimen from Samos (Hbra1) plots in the upper right portion of the Höwenegg ellipse along with Pikermi specimens.

Fig. 10 includes Log 10 ratio diagrams of MTIII. Fig. 10a compares Baccinello V3 IGF 8193V (Plate 1, fig. 3) to a suite of Vallesian aged European and Turkish
MTIII. The oldest and most primitive of the Central European hipparions is the Inzersdorf *Hipparium primigenium* which has a relatively shorter MTIII (M1) with particularly small proximal articular depth (M6) dimensions and minimal M3 versus M4 midshaft “Esme Acakoy-like” dimensions Scott et al. (2005a) argued that the Inzersdorf *Hipparium* is a primitive member of the genus and reflects the primitive morphology. Turkish *Cormohipparion sinapensis* from Esme Acakoy is somewhat younger (10.5 Ma; Bernor et al., 2003b) than the Inzersdorf ‘hipparion, having a greater maximum length dimension (M1) than Inzersdorf, but exhibiting the same modest M3 versus M4 contrast as seen in the Inzersdorf *Hipparium*. Rudabanya *Hipparium intrans* has a very long maximum length (M1) and very wide midshaft (M3) compared to its midshaft depth (M4). While being shorter than *H. intrans*, Dinotheriensandes *Hipparium primigenium* (mean) measurements reflect the same
elevated M3, and proportionally lower M4 dimensions of *H. intrans* and has large proximal articular (M5 and M6) and distal articular (M10-M14) dimensions being a large population of *Hippotherium primigenium*. Baccinello V3 MTIII most closely tracks the Esme Acakoy Mean measurements, having particularly similar M1 proportions but accentuated narrow M3 versus deep M4 proportions. The length of these two taxa MTIII’s are very similar to the Höwenegg sample mean.

Fig. 10b plots IGF 8193V MTIII compared to Turolian members of the *Hippotherium* clade. Here, Baccinello’s overall profile is most similar to Baltavar *Hippotherium microdon*, but Baccinello V3 has mostly larger and longer MTIII. In turn, Baccinello V3 most closely resembles the Polgardi mean population differing mostly in Polgardi’s larger dimensions of M3-M12 and M14. Pikermi MTIII is very similar to Höwenegg *Hippotherium primigenium*. Baltavar *Hippotherium intrans* is elongate and has robust midshaft proportions. Akkasdagı and Samos Hbra2 (*Hippotherium “brachypus”) have longer MTIII’s than Baccinello V3 and Höwenegg but are remarkable for their robust midshaft and articular measurements: they are tremendously robust. Our analysis suggests that Baccinello V3 *Hippotherium malpassii* n. sp. is most closely related to Central European *Hippotherium microdon* and Polgardi, and in turn are derived from *Hippotherium primigenium*. Our analysis further suggests that Pikermi *Hippotherium brachypus* is also closely related to Central European *Hippotherium primigenium*.

Fig. 11 includes a 1PHIII plot of maximum length (M1) versus proximal articular width (M4). Again, most of our sample plots within the Höwenegg ellipse, including several specimens from Rudabánya (r) and Eppelsheim (e). There is 1 specimen from Baltavar (t) plotted within the ellipse and 1 below and 1 far to the left of the ellipse. The single Sinap (s) specimen plots below the ellipse close to a specimen from Eppelsheim (e) and another from Rudabánya (r). There are 4 Baccinello V3 specimens plotted within the ellipse and two below the ellipse. The two largest specimens, IGF 9390V (Plate 1, fig. 4) and NHMB JH “nonumb” (=not numbered) group amongst the largest Rudabánya specimens, while two more plot lower in this ellipse; all of these 4 specimens are referable to *Hippotherium malpassii*. There is yet another group of Baccinello V3 specimens (IGF nonumb & NHMB JH 151) that are amongst the smallest in our sample at the bottom and below the bottom of the ellipse. There are yet specimens that are below the ellipse that may be of another taxon (NHMB JH 129, IGF 8194V and IGF 9392V, Plate 1, figs 5-6).

Fig. 12a includes Log 10 ratio diagrams of 1PHIII of Baccinello V3 specimens IGF 8194V, IGF 9390V, IGF 9392V, NHMB JH 129, NHMB JH 158 and NHMB JH nonumb1. The log10 ratios are generally similar to one another with 3 specimens, IGF 8194V, NHMB JH 129 and IGF 9392V diverging from the other 4 in their shorter length measurements (M1 and M2) and IGF 9392V being smaller yet in its proximal articular measurements (M5) and distal tuberosity (M6) measurements. Fig. 12b includes 1PHIII from Dorn Dürkheim, Germany (MN11), Baltavar, Hungary (MN12), the Dinotheriensandes, Germany (MN9) and Rudabánya, Hungary (MN9). Interestingly, the smallest of this sample from Dorn Dürkheim and Baltavar compare most closely with the smaller specimens from Baccinello V3. The larger two from Rudabánya and the Dinotheriensandes compare most closely with Höwenegg and the single intermediate specimen, NHMBJH158 from Baccinello V3. The two largest Baccinello V3 specimens IGF 9390V and NHMB JH nonumb1 are longer and have greater proximal articular widths than the entire remainder of the sample under consideration. These results are not strongly conclusive about Baccinello V3 1PHIII, but there seems to be a larger form, *Hippotherium malpassii* n. sp., likely represented by IGF 9390V, NHMB JH nonumb1 and NHMB JH 158, with IGF 8194V, NHMB JH 129 and IGF 9392V possibly representing a smaller taxon. As such, *Hippotherium malpassii* would appear to be advanced in the elevated length, proximal (M5 and M6) and distal (M7) articular measurements compared to other members of the Central European *Hippotherium primigenium* clade (H. *primigenium*, H. *intrans* and H. *microdon*).

The bivariate plots and Log 10 plots support a number of conclusions about the Baccinello V3 hipparions. The P3 occlusal width (M3) versus occlusal length (M1) plot (Fig. 4a) suggests that the Baccinello V3 hipparion is somewhat smaller than German Vallesian *Hippotherium primigenium* and compares in size to the Baltavar, Hungary hipparions. The P1 protocone width (M11) versus length (M10) plot demonstrates that the protocones are generally shorter and more rounded than in the Vallesian hipparions, comparing closely with the Baltavar, and apparently the Hatvan, Hungary hipparions. The astragalus plot (Fig. 5) demonstrates that the Baccinello V3 hipparion groups in the lower part of the ellipse with Eppelsheim, Rudabánya, Polgardi, Inzersdorf and Gaiselberg, with the Baltavar sample being smaller yet. Baccinello’s calcaneum
(Fig. 6) maximum length (M1) versus maximum width (M6) is small compared to most of this sample, and in particular German Vallesian hipparions. Baccinello V3 MCIII (Fig. 7) compares well in its maximum length (M1) versus distal articular width (M11) with Esme Acakoy, Inzersdorf, Sinap and much of Baltavar plotting together in the lower part of the Höwenegg ellipse. Baltavar has the smallest MCIIIs of the sample. The MCIII Log10 ratios (Figs 8a, b) reveal that Baccinello V3 *Hippotherium malpassii* compare most closely with Turolian members of the clade from Polgardi, Baltavar and Dorn Dürkheim. The MTIII bivariate plot (Fig. 9) again has Baccinello V3 plotting on the lower left border of the ellipse close to the Baltavar hipparion. The MTIII Log 10 ratio plot (Fig. 10b) shows a close comparison between the Turolian hipparions from Baltavar and Polgardi. The 1PHIII bivariate plots (Fig. 11) suggest two taxa at Baccinello V3 and this is reinforced by the log10 ratio plots (Figs 12a,b), with the larger sample being referable to *Hippotherium malpassii*. In conclusion, Baccinello V3 *Hippotherium malpassii* n. sp. compares most closely with Hungarian (Baltavar and Polgardi) species of *Hippotherium*, and is readily derived from Central European *Hippotherium primigenium*. 

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Fig. 12 - Log 10 ratio diagrams of **1PHIII.** Fig. 12a includes Log 10 ratio diagrams of **1PHIII** of Baccinello specimens. Fig. 12b includes **1PHIII** from Baccinello V3 and Dorn Dürkheim, Germany (MN11), Baltavar, Hungary (MN12), the Dinothiersandes, Germany (MN9) and Rudabánya, Hungary (MN9).
SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA Owen, 1848
Suborder HIPPOPOMORPHA Wood, 1937
Superfamily EQUOIDEA Hay, 1902
Family EQUIDAE Gray, 1821
Subfamily EQUINAE Steinmann & Doderlein, 1890

Hippotherium malpassii n. sp.

Derivatio nominis - Named in honon of the late Nedo Malpassi (Firenze) as a tribute to his long and enthusiastic survey activity in the Baccinello-Cinigiano area.

Holotype - IGF 9400V - Right maxillary I¹-I³, left maxillary P²-M³ (Fig. 13).

Hypodigm - See Tab. 2.

Other referred specimens - See Tab. 2.

Type Locality - Badlands south of Podere Firenze, Baccinello-Cinigiano Basin, Arcidosso, Tuscany, Italy. UMTS coordinates 32TE693975 N4746299 (Fig. 1).

Age - Latest Miocene, Messinian Stage. The sedimentary succession outcropping south of Podere Firenze, is lithostratigraphically correlated with the Ribaldella log (Fig. 3), paleomagnetically calibrated to the C3An.2n Chron, bracketed between 6.733 and 6.436 Ma (Rook et al., 2011). Baccinello V3 Faunal Unit. MN13 zone in the European Mammal Biochronological scale.

Diagnosis (autapomorphies in this lineage compared to Hippotherium primigenium are in italics) - A moderate sized member of the Hippotherium lineage distinguished by having the skull with a long preorbital bar and lacrimal extending approximately ¾ of the distance from the anterior orbital rim to the posterior rim of the preorbital fossa. The preorbital fossa has moderate medial depth, only slight posterior pocketing and a weakly defined anterior rim (all known only in a single juvenile skull). Adult maxillary cheek teeth are extremely richly plicated, including even the anterior margin of the prefossette; pli caballins are richly and complexly ornamented; protocones varying from short ovals to small rounded morphology; hypoglyphs often only moderately deeply incised. Mandibular cheek teeth with substantially larger metaconid than metastylid with an elongate isthmus separating them; pre- and postflexids are very complex. Permanent cheek teeth with a maximum crown height approximately 55 mm. Deciduous maxillary cheek teeth have small, rounded protocones. Deciduous mandibular cheek teeth have sharply reduced to absent ectostylys. Metacarpal III and metatarsal III are elongate-slender in morphology, otherwise close in size to H. primigenium and larger than H. microdon. The I¹ phalanges III are similar to, but more slender than H. primigenium; astragali and calcanea are generally the size of H. primigenium and larger than Baltavar (Hungary) Hippotherium microdon.

Description - The Holotype IGF 9400V includes a right maxillary I¹-³ and left maxillary P²-M³ (Fig. 13). The incisors are worn and unremarkable in their morphology.

Fig. 13 - Hippotherium malpassii n. sp. Holotype from Arcidosso (Podere Firenze). IGF 9400V, left maxillary dentition (P²-M³) in a) labial, and b) occlusal views. Scale bar represents 5 cm.
Tab. 2 - List of studied *Hippotherium* material from Baccinello-Cinigiano Basin “V3” localities.
P2 has anterostyle elongate, pre- and postfossette borders are extremely complex, including the mesial and lingual borders of the prefossette, which is unusual; pli caballin is richly ornamented having 5 individual plis; protocone has a distinct mesial pli, primitive for Old World hipparion, and has a short oval shape overall; hypoglyph is moderately deeply incised, an autapomorphy for the *Hippotherium* lineage. P3’s morphology is as in P2, lacking anterostyle, lacking a pli on the protocone and having pli caballin with 8 individual plis; P4 is as in P3 except that the pli caballin has 3 individual plis; M1 is the most worn tooth in the row, and as a result the pre- and postfossette plis are shorter, but still show the same level of complexity as the premolars, including on the mesial border of the prefossette, the remaining morphology is the same as in the premolars except the pli caballin which has 4 plis; M2 and M3 differ from M1 in having shorter, rounded protocones, both have complexly ornamented pli caballins which defy an accurate count and M3 is the only cheek tooth with a deeply incised hypoglyph that does not quite surround the hypocone.

There are a number of localities that preserve maxillary cheek teeth that are similar to the type specimen. Amongst these, the most important is Ribaldella (also referred as “Ribardella”) which also preserves rare, com-
complete postcranial material. IGF 9406V and IGF 9407V (Figs 14a and 14b) are a left M$_1$ and M$_2$, respectively, and both are just beyond their middle stage-of-wear. Both of these specimens are similar to the Type $H$. malpassii in several morphologic features: the fossettes are extremely complex, and in the case of the M$_1$, the prefossette even has a complex lingual margin and both the mesial border of the prefossette and the distal border of the postfossette are very complex. In both, there are multiple (3) pli caballins on both teeth. The protocone is elongate oval in both, being less rounded than in the type specimen. Hypoglyph is moderately deeply incised on the M$_1$ and more deeply incised on the M$_2$. The morphological details of these two specimens secure their inclusion in the hypodigm of $Hippotherium$ malpassii.

The locality of Scansano “1-3” has dental material that shares a number of similarities to the type specimen. NHMB JH 126 includes a number of closely associated specimens: NHMB JH 126A, a right P$_3$; NHMB JH 126B, a left P$_3$; NHMB JH 126C, a left M$_1$; NHMB JH 126D, a left M$_2$; NHMB JH 126E, a right P$_3$; NHMB JH 126F, a left P$_4$. These teeth are similar to the type specimen in all regards except the protocone presents as mostly a slightly smaller, round structure (Fig. 15a-f). Another Scansano specimen, NHMB JH 126E, a right P$_3$, is identical to the Type specimen P$_3$ in all regards including the primitive (and often rare) occurrence of a mesial pli. Scansano “1-3” also has some lower cheek teeth that we refer to $H$. malpassii. NHMB JH 133 (Fig. 16a-b) is a left P$_4$ characterized as having: metaconid and metastyloid large and oblong-shaped, pre- and postflexids with complex margins, pli caballinid double, protostyloid absent on the occlusal surface, and very small rounded structure on the mesiolabial wall of the tooth.

The locality of Scansano Pod. S. Croce has a left P$_4$ in early wear (NHMB JH 134; Fig. 17a-b) that also exhibits the morphologic hallmarks of $Hippotherium$ malpassii. This specimen has a mesostyle crown height of 44.3 mm, and given that it is in early wear, one would not expect the crown to have had an original unworn height of more than 50 mm. This is a primitive feature for Old World hipparions. Other salient morphological characters typical of $H$. malpassii n. sp. include: protocone is a small rounded structure and hypoglyph is only moderately deeply incised. Due to the early stage-of-wear, the plications are not as developed as in the type specimen, but one can see that the pli caballin is already complex and the mesial border of the prefossette is beginning to express complexity not found in most hipparion taxa.

A Roccalbegna (Fosso del Taffone) specimen, NHMB JH 140, is a right P$_2$ in an advanced stage-of-wear (crown height=13.2 mm). As expected this specimen has a larger rounded protocone and plications are diminished. Still, while the pre- and postfossettes have become labio-lingually more restricted, there remains complex plications on the mesial and distal borders of the prefossette and the mesial border of the postfossette. Taking into account this specimen’s advanced stage-of-wear, it has a completely expected occlusal morphology for $H$. malpassii.

Arcidosso “11” (type locality) has specimens that are included in the hypodigm of $Hippotherium$ malpassii. NHMB JH 229 includes 5 associated maxillary cheek
teeth: NHMB JH 229A, a right P3; NHMB JH 229B, a left P3; NHMB JH 229C, a left M1; NHMB JH 229D, a right P2; NHMB JH 229E, a left P4. The right P2 (NHMB JH 229D, Fig. 18a-b) is similar to the type Hippotherium malpassii in its extremely complexly plicated fossettes at their apices. Likewise, the anterostyle is elongate, the hypoglyph is moderately deeply incised and the protocone is oval-shaped, but lacks a mesial pli. NHMB JH 229A and NHMB JH 229B, right and left P3's (respectively), would appear to be somewhat higher crowned than the type for its stage-of-wear, but retains characteristic morphologic features of H. malpassii including complex plications of the pre- and postfossettes and multiple (4) pli caballins. They both differ however from the type specimen in having an elongate-oval protocone and very deeply incised hypoglyph, this last feature perhaps being due to their early stage-of-wear. The left M1, NHMB JH 229C is the most worn of these teeth (crown height = 41.9 mm), and it exhibits extremely complexly ornamented plications of the pre- and postfossettes and the pli caballin (Fig. 19a-b). The pli caballin nearly defies description in that there are two main trunks with several small plis emanating from the borders. As in the previously described NHMB JH 229 specimens, the hypoglyph is deeply incised and the protocone is elongate oval. The left P4, NHMB JH 229E has all of the salient features described above for the two P3's.

Arcidosso “1-2”, a site located 1.5 Km NE of the type locality, has yielded a complete right mandibular dentition, NHMB JH 160A-F (note these are serially labeled from P2-M3, but P3 and P4 have been reversed so that P1 is NHMB JH 160C and P1' is NHMB JH 160B; Fig. 20). The mandibular P3 (NHMB JH 160B) has the highest crown, 49.6 mm., which given the full expression of its occlusal morphology, and for that matter the full expression of M1's occlusal morphology, suggests that it had a maximum unworn crown height was in excess of 50 mm. In itself, this suggests that the Arcidosso “1-2” hippo- rion was slightly advanced in its crown height compared to the Type specimen of Hippotherium malpassii. The crowns of all these specimens are worn, but obviously not in a middle stage-of-wear where occlusal features are characteristically expressed. The metaconids and metastylids are essentially as in the Type specimen and specimens referred to H. malpassii above, but the pre- and postflexids do not have complex margins and the pli caballinid is not expressed on the occlusal surface. This leads us to refer the Arcidosso dental sample to Hippotherium aff. malpassii.

There is a juvenile skull and mandible, IGF 5286V in the Florence collection that is derived from the Roccalbegna “Podere le Pigne” locality. The skull (Fig. 21) is complete except for the snout and posterior cranium and has right and left dP2-M3 with M1's apparent in its crypts. The labial view of the skull shows a clear, triangular shaped POF with a long preorbital bar. There is a separation of the skull along the lacrimal suture that is well posterior to the POF. The POF itself has medium depth, only slight posterior pocketing, moderate medial depth and a prominent ventral and less prominent anterior rim and is placed well above the facial-maxillary crest. The
IOF is found above the limit between $dP^2$ and $dP^3$. The $dP^2$ is in early wear with only the opposing borders of the pre- and postfossettes showing some plications; the anterostyle is elongate, pli caballins are weakly double, protocone is small and rounded. The $dP^3$ and $dP^4$ are rectangular shaped, plications are only complex on the distal border of the prefossette, being less complex on the mesial borders of the postfossettes and simple on the mesial border of the prefossettes and distal border of the postfossette; protocones are as in the $dP^2$. The hypoglyphs are very deeply incised, encircling the hypocones on all deciduous cheek teeth. The juvenile mandible includes

Fig. 21 - *Hippotherium malpassii* n. sp. from Roccalbegna (Podere le Pigne). IGF 5286V, juvenile skull in left lateral (a) and basal (b) views. Scale bar represents 5 cm.
dP₂₃ with M₁ emerging from its crypt. The teeth are as in the maxillary dentition being in early wear. Salient morphological features include: metaconids are generally rounded while metastylids are more square-shaped; pre- and postflexids are poorly developed; ectoflexids are deep separating metaconid and metastylid.

Remarks - Baccinello V3 Hippotherium malpassii n. sp. is a late Turonian (MN 13) species of the Hippotherium lineage. The facial morphology is similar to Vallesian members of the clade except for some reduction in the height and depth of the POF as judged from a single juvenile specimen. The dentition exhibits even greater complexity of the pre- and postfossettes and number of pli caballins than Central European Vallesian hipparions (Bernor et al., 1988, 1997; Woodburne, 2007). Protocone pli caballins than Central European Vallesian hipparions (Bernor et al., 1988, 1997; Woodburne, 2007). Protocone morphology differs from Vallesian members and compares closely with Turolian members of the clade. Koufos & Vlachou (2005) Vlachou & Koufos (2009) have shown in particular Turolian members of the clade. Koufos & Vlachou (2005) Vlachou & Koufos (2009) have shown that “Hipparion” (= Hippotherium to us) brachypus from Akkasdagi, Turkey as well as Pikermi and Samos, Greece has many of the skull features of Hippotherium but is larger, has a longer snout and has more massive metapodials than the Central European members of the clade and Pikermi H. brachypus s.s. We accept the comparisons of these Greek species and include Pikermi H. brachypus and Samos and Akkasdagi H. “brachypus” within the Hippotherium clade.

Our current understanding of the Hippotherium clade’s historical biogeography is that it is derived from North American Cormohipparion, its oldest known occurrence being in the Vienna Basin (Bernor et al., 1988, 1996; Woodburne, 2007). Central European Hippotherium is the sister taxon of Turkish Cormohipparion sinapensis. Earliest Hippotherium sp. is known from the Pannonian Basin of Austria and Hungary. By the medial Turolian, the clade had extended its range as far as Greece and Turkey to the South and East as well as Tuscany to the south and west. The origin of the Italian Hippotherium malpassii n. sp. would best be posited as being the western Pannonian Basin with Baltavar, Polgardi and Hatvan all having hipparions that are morphologically very similar to the Baccinello V3 hipparion. Pikermi Hippotherium brachypus is found herein to compare closely with German Vallesian Hippotherium primigenium, particularly in metapodial proportions. Samos and Akkasdagi Hippotherium “brachypus” (our Hbra2) are related to

C and already shows complex plication amplitudes of the fossettes and pli caballins. Maximum crown height would appear to have been near 55 mm and MPIIs were not as large as in later Vallesian hipparions from Eppelsheim and Höwenegg, Germany (Scott et al., 2005a). Hippotherium had a demonstrated Vallesian age distribution that included Central Europe: Germany and the greater Pannonian Basin of Austria and Hungary. By the medial Turolian, the clade had extended its range as far as Greece and Turkey to the South and East as well as Tuscany to the south and west. The origin of the Italian Hippotherium malpassii n. sp. would best be posited as being the western Pannonian Basin with Baltavar, Polgardi and Hatvan all having hipparions that are morphologically very similar to the Baccinello V3 hipparion. Pikermi Hippotherium brachypus is found herein to compare closely with German Vallesian Hippotherium primigenium, particularly in metapodial proportions. Samos and Akkasdagi Hippotherium “brachypus” (our Hbra2) are related to
Pikermi Hippotherium brachypus, being derived in its increased size and greater massivity of the postcaninials. The Greek and Turkish specimens of the Hippotherium brachypus clade were likely vicariant from Central European and Italian Hippotherium by the early Turolian. Fig. 22 provides a biogeographic summary of the Central European MN 9 origin of the Hippotherium clade, its extension into Greece and Turkey by MN12 and the extension of MN13 Hippotherium from the Pannonian Basin into Tuscany.

**PALEODIETARY RECONSTRUCTION**

**Mesowear Analysis**

**Introductory Considerations** - The mesowear method, initially developed by Fortelius & Solounias (2000) has proven to be a powerful tool for reconstructing paleodietary adaptations (Kaiser et al., 2000). The mesowear method is based on facet development of cheek tooth occlusal surfaces. The degree of facet development reflects the relative proportions of tooth-to-tooth contact (attrition) and food to tooth contact (abrasion). Attrition creates facets while abrasion obliterates them. The entire exposed surface of a tooth is affected by wear, but mesowear analysis so far has focused on the cutting edges of cheek tooth enamel surfaces where the buccal wall (ectoloph in perissodactyls) meets the opposing edges of cheek tooth enamel surfaces. The mesowear variables of the type specimen of Hippotherium primigenium (IGF 9400V) is an upper cheek tooth row, and 4 teeth (P4, M1, M2 and M3) are analyzed (DS 6).

**Results and Dietary Interpretation** - Mesowear frequencies and calibration factors are given in Table 3 following the methodology of Kaiser & Solounias (2003) and Kaiser & Fortelius (2003). The cluster diagram (Fig. 23) illustrates the relationships between the datasets. The closer the data, the smaller the Euclidean distance (ED) at the branching point. The dendrogram shows four main clusters. Cluster 1 represents the most abrasion dominated feeding traits among grazers; cluster 2 comprises several grazers with less abrasive diets. Cluster 3 contains the intermediate-feeders, and cluster 4 corresponds to the attrition-dominated end of the dietary spectrum and contains browsers only. The two datasets of Hippotherium malpassii (Himal-BA) are positioned in the cluster 2 together with the Eppelsheim population of H. primigenium and appear closest to the extant African grazing antelopes Kobus ellypsiprymnus, Redunca redunca, Hippotragus equinus and Hippotragus niger. The waterbuck, Kobus ellipsiprymnus, clusters closest with Hippotherium primigenium (Eppelsheim) and Hippotherium malpassii. The waterbuck frequents reedbeds and shrubby growth and also forage into woodlands. The animals, however, usually live in proximity to water (Nowak, 1999). According to Kingdon (1982) the major sources of food are medium and short grasses like Andropogon, Brachiaria, Cenchrus, Chloris, Cynodon, Cyperaceae, Cymbopogon, Dichrostachys, Digtaria, Heteropogon, Haparrhenia and Panicum species, reeds and rushes (Phragmites and Typha). To a lesser extent browse like leaves and fruit are eaten (Kingdon, 1982). Based on cluster analysis, the prevailing dietary regime of the Baccinello V3 hippoassembly is therefore suggested to be equivalent to that of the waterbuck.

Principal components analysis (PCA; Fig. 24) plots the Baccinello V3 bulk sample (Himal-BA-txm) of Hippotherium malpassii in the transitional factor space between the intermediate-feeders in kernel 3 and the less abrasion dominated grazers (kernel 2). We realize that within the factor space H. malpassii is slightly closer to the intermediate-feeder kernel (k3), where in fact the African impala (Aepyceros melampus) would be the closest analogue species in terms of the mesowear signature. The impala is an ecotone species living in

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<td>0.00</td>
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<tr>
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<td>0.11</td>
<td>2.36</td>
<td>0.00</td>
<td>2.88</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>tx+tm (C/Hp)</td>
<td>4.11</td>
<td>18.36</td>
<td>4.00</td>
<td>14.88</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>Tx+tm (C/Hp) [%]</td>
<td>18.29</td>
<td>81.71</td>
<td>21.19</td>
<td>78.81</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>tx (IGF9400V-BA only)</td>
<td>0</td>
<td>100</td>
<td>25</td>
<td>75</td>
<td>0</td>
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</table>

Tab. 3. Absolute and calibrated mesowear scorings (datasets 1-6). DS = #of dataset, tx = maxillary tooth, tm = mandibular tooth, l = low occlusal relief, h = high occlusal relief, s = sharp cusp, r = round cusp, b = blunt cusp. DS 1 = absolute mesowear counts maxillary teeth. DS 2 = absolute mesowear counts mandibular teeth. CF<sub>n</sub> = Calibration factor for lower teeth of hipparionines as established for Hippotherium primigenium by Kaiser & Fortelius (2003). DS 3 = absolute mesowear counts of mandibular teeth calibrated by CF<sub>n</sub>. DS 4 = sum of calibrated counts in upper and lower teeth. DS 5 = calibrated frequency (percentage) used for analysis. DS 6 calibrated frequency (percentage) of mesowear variables of the type specimen of Hippotherium malpassii (IGF9400V-BA).
light woodland with little undergrowth and grassland of
low to medium height. The impala is found frequently
in grass dominated open environments like bushland
and Acacia savannahs but also in Acacia forests and
other deciduous woodlands. Impalas live near water
and shift feeding from grazing to browsing depending on
the season (Estes, 1991). Aepyceros melampus has a
diet that may be considered to be a perfectly balanced mixed
diet. The status of the impala as an intermediate-feeder
is uniformly acknowledged by all workers who have
evaluated ungulate dietary classifications (Janis, 1988;
Janis & Erhardt, 1988; Hofmann, 1989; Van Wieren,
1996; Fortelius & Solounias, 2000; Gagnon & Chew,
a grass/browse ratio of 60/40% based on Breymeyer &
Van Dyne (1980) and Skinner & Smithers (1990). Based

Fig. 23 - Hierarchical cluster diagram comparing a set of 27 "typical" extant species from Fortelius & Solounias (2000) with the Baccinello V3 samples of Hippotherium malpassii “IGF9400V-BA” and “Himal-txtn” (set bold). Distance = normalized Euclidean distance (root-
mean-squared difference). Circle = extant browser, rectangle = extant intermediate-feeder, triangle = extant grazer. Cluster 1 represents the most abrasion dominated feeding traits among grazers; cluster 2 comprises several grazers with less abrasive diets. Cluster 3 contains the intermediate-feeders, and cluster 4 corresponds to the attrition-dominated end of the dietary spectrum and represents browsers only. Comparative
datasets for fossil Old World Hippotherium are: Hippotherium primigenium from Eppelsheim (Hipri-EP; Kaiser, 2003), Hippotherium primigenium from Höwengegg (Hipri-HO; Kaiser, 2003), Hippotherium aff. primigenium from MN11 of Dorn-Dürkheim (Hipri-DD; Kaiser et al., 2003), Hippotherium kammerschmitiae from Dorn-Dürkheim (Hikam-DD; Kaiser et al., 2003), Hippotherium sumengense (Hisum-SU; Bernor et al., 1999), Hippotherium “microdon” from Baffiavar (MN 12; Himic-BA; Kaiser & Bernor, 2007) and Hippotherium intrans from Rudabanya (Hiint-RU; Bernor et al., 2003).
on stable isotopes Sponheimer et al. (2003) found a C4 grass ration of 51% in the Southern African population of *A. melampus* and 54% in the East African population of the species. Based on faeces, Codron et al. (2005) suggest a grass/browse ratio of 50/50% for *A. melampus*. Among the extant comparison species the impala is the only that consistently eats substantial amounts of grass. The remaining intermediate-feeders in this comparison have far less extensive grass components in their diets. The impala has therefore the most abrasive diet among all &0%E0#)0-/,./1)+/-PH//1/,9#+01#)9#3%09)9-/0-5?#35+99)B/1# next to the grazers in all mesowear evaluations.

and \(H.\) \textit{kammerschmittae} from Dorn-Dürkheim (Hikam-DD) are the only populations that classify in the browser kernel (k4).

We thus consider it likely, that Baccinello V3 \textit{Hippotherium malpassii} had a very similar diet as Baltavar \textit{Hippotherium} “\textit{microdon}” which was not very different in the proportion of abrasive agents as compared to the impala’s diet. Eppelsheim \(H.\) \textit{primigenium} also had a more abrasive dominated diet. It is remarkable, that all other Old World hipparion assemblages [\textit{Hippotherium samegenese} (Bernor et al., 1999), \textit{Hippotherium kammerschmittae} and \(H.\) \textit{primigenium} from Dorn-Dürkheim (Kaiser et al., 2003), \(H.\) \textit{primigenium} from Höwenegg (Kaiser, 2003), and \(H.\) \textit{intrans} from Rudabanya (Bernor et al., 2003a)] had diets corresponding to the intermediate feeding and browsing part of the dietary spectrum. Our work on paleodiet suggests that \textit{Hippotherium malpassii} was a mixed feeder not as committed to browsing as many Central European species of \textit{Hippotherium}, but similar to others such as Eppelsheim, Germany \textit{Hippotherium primigenium} and Baltavar, Hungary \textit{Hippotherium microdon}.

\section*{Isotopic analysis}

Carbon and oxygen stable isotopic analyses of tooth enamel can be informative for reconstructing paleodiet and paleohabitats. Carbon isotopes distinguish between diets of graze (\(C_4\) grasses and sedges) and browse (\(C_3\) plants such as trees and shrubs) due to differences in photosynthetic pathways between \(C_4\) and \(C_3\) plants. Additionally, plants yield a wide range of carbon and oxygen isotopic values in response to differences in irradiance and water stress and can therefore be useful in distinguishing closed canopy forests, woodlands, and open habitats. Increasingly open habitats, where plants are under high stress, yield the highest carbon and oxygen values. Isotopic values of tooth enamel reflect the values of plants eaten and water drunk by an individual during tooth development. Thus isotopic analyses of fossil teeth are useful in reconstructing an extinct species’ diet and habitat. Additionally, oxygen isotopes can be used in reconstructing paleoclimes, for water sources such as rivers and lakes respond to seasonal fluctuations in precipitation and temperature. Hypsodont equid teeth that take over a year to develop can be sampled multiple times along the length of the tooth to capture annual seasonal variability in oxygen isotopes, and hence reflect the degree of seasonality in that paleoenvironment. δ

We sampled a single \textit{Hippotherium malpassii} tooth, \(P^1\) IGF 9400V, three times from crown to root. After standard treatment, isotopic ratios are presented in the per mil (‰). In modern habitats, carbon values below -13‰ represent closed forests (Quade et al., 1995), Miocene carbon values are enriched by 1.5‰ relative to modern values due to changes in the atmosphere since the industrial revolution (Marino & McGlone, 1991). Therefore, carbon values of -12‰ or lower in the Miocene record are indicative of forest habitats. The δ\(^{13}\)C values for the three Baccinello V3 samples all fall below this cutoff, ranging from -13.2‰ to -12.6‰. The δ\(^{18}\)O values ranged from -3.6‰ to -3.1‰, for an intra-tooth range of 0.5‰. As a comparison, equid teeth from the Miocene Siwaliks of Pakistan exhibit oxygen ranges of approximately 2.5‰ per tooth, reflecting a seasonal environment comparable to a monsoon forest (Nelson, 2005). The small range for the Baccinello V3 \textit{Hippotherium malpassii} tooth suggests either a considerably less seasonal rainfall and temperature regime, or alternatively more permanent, buffered water sources that reflect the average annual precipitation isotopic values rather than the full range. Combined, the carbon and oxygen values of this equid tooth are consistent with a forest-dweller in a mesic environment.

\section*{CONCLUSIONS}

The Baccinello V3 faunas include a dominant, moderately large hipparion which we refer to \textit{Hippotherium malpassii} n. sp.

Our study of the Baccinello V3 hipparion provides us new insights into the \textit{Hippotherium} clade and its members. We agree with previous researchers that \textit{Hippotherium} originated in Central Europe following the immigration of North American Cormohipparion (Bernor et al., 1996; Woodburne, 2007). \textit{Hippotherium} underwent a modest evolutionary radiation in Central Europe between 11.2 and approximately 8 m.y. Species of Central European \textit{Hippotherium} were adapted to living in rich mesophytic forests and grassy woodlands with subtropical to warm temperate climate (Bernor et al., 1986) and adapted to mixed locomotor strategies that included running and leaping and springing (Bernor et al., 1997).

The Vienna and Pannonian Basins included the richest diversity of \textit{Hippotherium} species including: \(H.\) \textit{primigenium}, \(H.\) \textit{intrans} and \(H.\) \textit{microdon} (Bernor et al., 1993a,b; Bernor et al., 2003a; Scott et al., 2005a,b). The regional regression of the Central Paratethys in the Late Miocene established geographic connections from the Pannonian Basin southward through the Balkans to Greece. The Late Miocene faunas of Pikermi and Samos, Greece and Akkasdagi, Turkey included immigrant members of the \textit{Hippotherium} clade. We believe that the oldest member of this eastern Mediterranean - southwest Asian clade is \textit{Hippotherium brachypus} from Pikermi, Greece (Koufos, 1987a, b), which Bernor believes is circa 8 Ma. (Kostopolous & Bernor, in press). The Samos and Akkasdagi \textit{Hippotherium} is larger and has more massively built MPIIs and we believe likely to be a species derived from Pikermi \textit{Hippotherium brachypus}. This species would be younger than \textit{Hippotherium brachypus} being between 8 and 7 Ma.

Our paleoecological reconstructions demonstrate that Baccinello V3 \textit{Hippotherium malpassii} n. sp. remained tied to warm mesophytic subtropical woodland habitats into latest Miocene times. By the latest Miocene, hipparions had dispersed across all of Eurasia and Africa and included numerous clades, many of them being adapted to dry, seasonal open country habitats. Some of these in Africa and South Asia had shifted their dietary adaptation to eating coarse, C4 grasses and had adaptations strongly divergent from Central European \textit{Hippotherium}. Baccinello V3 represents the last known stand of the \textit{Hippotherium} lineage.
ACKNOWLEDGMENTS

For the access to collections, we thank B. Engesser and L. Costeur, curators of the Basel Naturhistorisches Museum and E. Ciuppi and S. Dominici, curators of the Florence Natural History Museum (Geology and Paleontology Section). The Baccinello collection housed at the Basel Naturhistorisches Museum has been increased since late 1950’s thanks to the precious and passionate work of the eminent paleontologist Prof. Johannes Hürzeler.

We deeply acknowledge M. Benvenuti and M. Papini (University of Florence), for their contribution to the geological mapping and understanding the sedimentary evolution of the Baccinello-Cinigiano basin, and Valerio Malpassi (Florence) for his painstaking field surveys in the Cinigiano area. Early phases of the preparation of this paper started in summer 2002, when L. Rook visited the Laboratory of Evolutionary Biology at Howard University (Washington DC, USA) holding a CNR-NATO Outreach Fellowship. This paper is based upon work supported by grants from the U.S. National Science Foundation under NSF Award (#BCS-0321893) to F.C. Howell and T.D. White (RHOI; Berkeley University), EAR0125009 to R.L. Bernor, and the University of Florence (Fondi di Ateneo) to L.Rook.

REFERENCES

Abbazzi L. (2001). Cervidae and Moschidae (Mammalia, Artiodactyla) from the Baccinello V3 faunal assemblage (Late Miocene, Late Turolian, Grosseto, Central Italy). Rivista italiana di Paleontologia e Stratigrafia, 107: 10-123.


Appendix – Baccinello V3 Hippotherium studied sample: measurement tables

**Table A1 - Upper Incisors**

<table>
<thead>
<tr>
<th>Specimen #</th>
<th>Species</th>
<th>element</th>
<th>side</th>
<th>M1</th>
<th>M2</th>
<th>M3</th>
<th>M4</th>
<th>M5</th>
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<tr>
<td>IGF 9400V</td>
<td>H. malpassii (Type)</td>
<td>I¹</td>
<td>R</td>
<td>15.6</td>
<td>-</td>
<td>10.6</td>
<td>-</td>
<td>-</td>
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<tr>
<td>IGF 9410V</td>
<td>H. malpassii</td>
<td>I¹</td>
<td>L</td>
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<td>10.4</td>
<td>9.6</td>
<td>-</td>
<td>22.0</td>
</tr>
<tr>
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<td>H. malpassii (Type)</td>
<td>I¹</td>
<td>R</td>
<td>14.1</td>
<td>-</td>
<td>8.7</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>IGF 9400V</td>
<td>H. malpassii (Type)</td>
<td>I¹</td>
<td>R</td>
<td>16.5</td>
<td>-</td>
<td>6.9</td>
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**Table A2 - Upper cheek teeth**

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<th>M5</th>
<th>M6</th>
<th>M7</th>
<th>M8</th>
<th>M9</th>
<th>M10</th>
<th>M11</th>
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<tbody>
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<td>H. malpassii (Type)</td>
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<td>L</td>
<td>32.5</td>
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<td>23.3</td>
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<tr>
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<td>H. malpassii</td>
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<td>R</td>
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<td>32.3</td>
<td>23.0</td>
<td>22.7</td>
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<td>H. malpassii</td>
<td>p1</td>
<td>L</td>
<td>-</td>
<td>22.2</td>
<td>22.6</td>
<td>17.1</td>
<td>4</td>
<td>7</td>
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<td>1</td>
<td>6.9</td>
<td>5.1</td>
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<tr>
<td>IGF 5286V</td>
<td>H. malpassii</td>
<td>p1</td>
<td>L</td>
<td>35.9</td>
<td>-</td>
<td>22.5</td>
<td>-</td>
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<td>3</td>
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<td>NHMB JH 43</td>
<td>H. malpassii</td>
<td>p1</td>
<td>L</td>
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<td>L</td>
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<td>23.6</td>
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<td>H. malpassii</td>
<td>p1</td>
<td>R</td>
<td>32.9</td>
<td>32.9</td>
<td>23.1</td>
<td>22.1</td>
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<td>R</td>
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<td>-</td>
<td>-</td>
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<td>-</td>
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<tr>
<td>IGF 9400V</td>
<td>H. malpassii (Type)</td>
<td>p1</td>
<td>L</td>
<td>24.3</td>
<td>20.4</td>
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<td>24.4</td>
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<td>H. malpassii</td>
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<td>R</td>
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</table>
M10 = crown height as measured from base to occlusal level on mesial face of the tooth.

**Table A3 - Lower cheek teeth**

- **M1** = length at occlusal level; **M2** = length 10mm above the tooth’s base; **M3** = length of metacodon-metastylid; **M4** = length of the prefossette; **M5** = length of the postfossette; **M6 = width across plane of ectoflexid/linguaflexid ;** **M7 = width 10mm above the tooth’s base;** **M8 = width across plane of metacodon and enamel band labial to protoconid;** **M9 = width across plane of metystylid and enamel band labial to hypoconid;** **M10 = crown height as measured from base to occlusal level on mesial face of the tooth.**

<table>
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<tr>
<th>Specimen #</th>
<th>Species</th>
<th>element</th>
<th>side</th>
<th>M1</th>
<th>M2</th>
<th>M3</th>
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<th>M6</th>
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<td>H. malpassii</td>
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<td>L</td>
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<td>L</td>
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**TABLE A4 - MANDIBLE**

M1 = maximum jaw length; M2 = muzzle length; M3 = premolar tooth row length; M4 = molar tooth row length; M5 = cheek tooth row length; M6 = length of ascending ramus; M7 = muzzle breadth; M8 = eight of mandible at condyle; M9 = eight of ascending ramus; M10 = eight of jaw posterior to M1; M11 = eight of jaw between P4 and M1; M12 = eight of jaw anterior to P4; M13 = length of the symphysis; M14 = minimum breadth of the symphysis.
### Table A5 – Forelimb elements

#### Humerus

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### Table A6 – Hindlimb elements

**Tibia**  
M1 = maximal length; M2 = medial length; M3 = minimal breadth; M4 = depth of diaphysis at level of M3; M5 = proximal maximal breadth; M6 = proximal maximal depth; M7 = distal maximal breadth; M8 = distal maximal depth.

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<th>M6</th>
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<th>M8</th>
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| IGF 9369V       | H. sp.  |      |    |    |    |    |    |    |    | 69.4 |}

**Astragalus**  
M1 = maximal length; M2 = maximal diameter of the medial condyle; M3 = breadth of the trochlea (at the apex of each condyle); M4 = maximal breadth; M5 = distal articular width; M6 = distal articular depth; M7 = maximal medial depth.

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<th>M7</th>
<th>M8</th>
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| IGF 2026V       | H. malpassii | R   | 56.7 | 55.1 | 25.8 | 52.5 | 42.1 | 31.9 | 42.4 |}
| IGF 8195V       | H. malpassii | L   | 56.9 | 55.1 | 24.6 | 53.0 | 42.1 | 32.3 | 41.9 |}
| IGF 9395V       | H. malpassii |     | 54.7 | 55.7 | 25.8 | 55.8 | 42.2 | 31.4 | 42.1 |}
| NHMB JH 149     | H. malpassii | R   | 55.0 | 52.4 | 25.0 | 56.5 | 42.6 | 30.8 |   |   |
| IGF 9396V       | H. sp.    | R   | 50.8 | 53.4 | 21.6 | 48.4 | - | - | - | - |
| NHMB JH 16      | H. sp.    | L   | 56.8 | 57.6 | 25.8 | 57.9 | 44.3 | 32.5 | - |   |
| NHMB JH 128     | H. sp.    | L   | 57.5 | 52.3 | 30.0 | 42.0 | 38.0 | 30.6 | - |   |
| NHMB JH 157     | H. sp.    | R   | -   | -   | -   | -   | 41.0 | 31.0 | - |   |
| NHMB JH 225     | H. sp.    | L   | -   | -   | -   | -   | 43.6 | 33.8 | - |   |

**Calcaneum**  
M1 = maximal length; M2 = length of the proximal part; M3 = minimal breadth; M4 = proximal maximal breadth; M5 = proximal maximal depth; M6 = distal maximal width; M7 = distal maximal depth.

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<th>M6</th>
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| NHMB JH 198     | H. malpassii | R   | 105.8 | 66.2 | 19.7 | 27.3 | 28.8 | 44.7 | 46.8 |}

**Naviculare**  
M1 = proximodistal diameter; M2 = mediolateral diameter; M3 = craniocaudal diameter.

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</table>

**Cuboid**  
M1 = maximum craniocaudal diameter; M2 = maximum proximodistal diameter; M3 = maximum mediolateral diameter.

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<th>side</th>
<th>M1</th>
<th>M2</th>
<th>M3</th>
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<td>H. sp.</td>
<td>R</td>
<td>26.9</td>
<td>36.8</td>
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</tr>
<tr>
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**Metatarsale III**  
M1 = maximal length; M2 = medial length; M3 = minimal breadth; M4 = depth of diaphysis at level of M3; M5 = proximal articular breadth; M6 = proximal articular depth; M7 = maximal diameter of the articular facet of the third tarsal; M8 = diameter of the articular facet for the fourth tarsal; M9 = diameter of the articular facet for the second tarsal; M10 = distal maximal supra-articular breadth; M11 = distal maximal articular breadth; M12 = distal maximal depth of the keel; M13 = Distal minimal depth of the lateral condyle; M14 = distal maximal depth of the medial condyle.

<table>
<thead>
<tr>
<th>Specimen number</th>
<th>Species</th>
<th>side</th>
<th>M1</th>
<th>M2</th>
<th>M3</th>
<th>M4</th>
<th>M5</th>
<th>M6</th>
<th>M7</th>
<th>M8</th>
<th>M9</th>
<th>M10</th>
<th>M11</th>
<th>M12</th>
<th>M13</th>
<th>M14</th>
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<tr>
<td>IGF 8193V</td>
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<td>33.0</td>
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### Table A7 – Phalanges

#### 1st Phalanx central digit (III)

<table>
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<th>M5</th>
<th>M6</th>
<th>M7</th>
<th>M8</th>
<th>M9</th>
<th>M10</th>
<th>M11</th>
<th>M12</th>
<th>M13</th>
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<tbody>
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<td><em>H. malpassii</em></td>
<td>L</td>
<td>67.0</td>
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<td>32.7</td>
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<tr>
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<tr>
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<td>L</td>
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#### 2nd Phalanx central digit (II and IV)

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#### 2nd Phalanx lateral digits (II and IV)

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<td>IGF 9391V</td>
<td><em>H. malpassii</em></td>
<td>L</td>
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<td>28.6</td>
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<td><em>H. sp. (small sized)</em></td>
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<td>42.1</td>
<td>31.4</td>
<td>31.8</td>
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</table>