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# PHYLOGENETIC SIGNATURES IN THE JUVENILE SKULL AND DENTITION OF OLDUVAI *EURYGNATHOHIPPUS CORNELIANUS* (MAMMALIA: EQUIDAE)

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*Abstract*. We describe and compare a *Eurygnathohippus* juvenile skull, RMNH67/5665 from site BKII, Olduvai Gorge, ca. 1.2 Ma. Study of the facial morphology and cheek tooth metrical data including length versus width and protocone length versus width of the dP2, 3 and 4 support the conclusion that this juvenile skull is the species *Eurygnathohippus cornelianus*, and that in turn *Eu. cornelianus* is a member of the "*Sivalhippus*" Complex, which includes the following superspecific clades: *Sivalhippus, Eurygnathohippus, Plesiohipparion* and *Proboscidipparion.* Recent studies suggest that *Eurygnathohippus* has a particularly close phylogenetic relationship with *Plesiohipparion.*

## Introduction

In his description of Miocene to Pleistocene Hipparions from Kenya, Tanzania and Ethiopia, Hooijer (1975) recognized an advanced hipparion from Olduvai Gorge and the Omo Group, "*Hipparion ethiopicum*" (and specifically "*Hipparion* cf. *ethiopicum*" from Olduvai Gorge) alongside a much smaller, dwarf form he referred to *Hipparion* aff. *sitifense*. Leakey (1965: pl. 20) recognized the derived morphology and identity of the larger Olduvai hipparion with the Cornelia, South Africa hipparion, "*Hipparion*" *cornelianum* (van Hoepen, 1971). Hooijer (1975) advanced his concept of the taxon "*Hipparion ethiopicum*" from Omo Shungura F, G, H, J, K and L. Hooijer (1975: plates 7-10) figured adult skull material from BK II (upper Bed II), Olduvai, and derived hypertrophied premaxillary incisors (Hooijer, 1975: plate 11) and mandibular incisors (Hooijer, 1975: plate 12) also from Olduvai BK II.

Armour-Chelu et al. (2006) found that the larger hipparion from Olduvai Beds I and II is justifiably referred to *Eurygnathohippus cornelianus* s.s. and that this advanced hipparion was likely related to the older Omo Shungura F, H and K *Eurygnathohippus* "*ethiopicus*" sensu Hooijer (1975). However, we believe that there is an outstanding issue with the taxonomic efficacy of *Eurygnathohippus* "*ethiopicus*" because it is not distinctly characterized by morphological features clearly separating it from *Eurygnathohippus cornelianus* s.s. as defined here and by Armour-Chelu et al. (2006). As noted for the hipparion derived from the Ndolanya beds of Laetoli (Armour-Chelu & Bernor 2011), there would appear to be advanced morphologies characterizing this clade beginning around the 2.7-2.5 Ma interval in eastern African hipparions that herald the origin of the *Eurygnathohippus cornelianus* lineage. New material emerging from the Omo and Middle Awash horizons in Ethiopia may yield further decisive resolution to this unresolved question.

As for the smaller hipparion from the Omo Shungura and Olduvai sequences, we follow Hooijer (1975) and Armour-Chelu et al. (2006) in recognizing that there is a second, smaller species of hipparion from the Omo and Olduvai Gorge between 2.3 and 1 Ma. However, this taxon is very rare and currently lacks sufficient skeletal material to be adequately diagnosed as a species. Hooijer's use of the nominal taxon "*Hip-*

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*parion*" aff. *sitifense* has been shown to be wholly inappropriate (re: Bernor & Harris 2003; Bernor et al. 2010).

The current work is intended to assess the morphologic and phylogenetic significance of RMNH67/5665, a juvenile skull from Olduvai Bed II, site BK II, housed by the Natural History Museum Leiden. This skull is mostly complete except for the nasals and premaxilla, and includes a well preserved deciduous dentition and M1. The occipital region is present but separate from the remainder of the skull. This specimen is clearly referable to the large Olduvai hipparion, *Eurygnathohippus cornelianus* s.s. This skull preserves a number of morphological features that provide important insights into its phylogenetic history. We report this set of observations and our conclusions about their significance here.

## Abbreviations

The juvenile skull is housed by the National Museum of Natural History (Naturalis), Leiden, the Netherlands.

M before a number refers to the measurement number defined by Eisenmann et al. (1988) and Bernor et al. (1997). Measurements on the skull are identical between Eisenmann et al. (1988) and Bernor et al. (1997) while measurements on cheek teeth explicitly follow Bernor et al. (1997). Definitions of measurements taken are included in the legend for Table 1. Bivariate plots of dP2-4 occlusal length (measurement 1) versus occlusal width (measurement 3) and protocone length (measurement 10) versus protocone width (measurement 11) have been made and assessed below for the Olduvai juvenile skull and a large data set following Wolf & Bernor (2013).

## 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. (1988, 1996, 1997) and Scott et al. (2005a and b). Bernor et al. (2010, 2011) updated these conventions in terms of anatomical and systematic nomenclature which we follow herein. Our use of a comprehensive data set for Old World hipparionine deciduous teeth is based on the analysis by Wolf & Bernor (2013). Recognition of the validity of the African hipparion genus *Eurygnathohippus* follows observations and analyses by Bernor & Armour-Chelu (1999); Bernor & Harris (2003); Armour-Chelu et al. (2006); Bernor et al. (2005); Bernor & Kaiser (2006); Bernor (2007); Bernor et al. (2008); Gilbert & Bernor (2008); Bernor & Haile-Selassie (2009); Bernor et al. (2010); Wolf et al. (2010); Armour-Chelu & Bernor (2011); Bernor et al. (2012); Melcher et al. (2013); Bernor et al. (2013); Bernor & Sun (in press).

## Morphological Observations and Comparisons - Description of Juvenile Skull RMNH67/5665

RMNH67/5665 is a juvenile skull with most of the facial region, orbit, braincase and palate including right dP2-M1 (the last exposed within its crypt) and left dP2-4 (Fig. 1A, C). There is no evidence of a dP1 having been present. Morphological features of the face include: preorbital fossa (POF) is shallow, but distinct; preorbital bar (POB) is long, being 56.3 mm. in length (M32); POF itself has a maximum length of 39.7 mm. (M33) and the length from the posterior rim of the POF to the distal rim of the infraorbital foramen (IOF) is 43.9 mm (M34); the height of the posterior aspect of the POF to the alveolar border of the maxilla is 77.4 mm (M38) (Tab. 1). The anterior-most projection of the lacrimal bone is less than ½ the distance from the anterior orbital rim to the posterior rim of the POF.

The maxillary cheek teeth on the right side include dP2-4 and M1 emerging from its crypt. The dP2 has an elongate anterostyle, parastyle is pointed, mesostyle is squared labially; prefossette is very elongate and complex on both its mesial and distal surfaces; postfossette is complex on its mesial surface, less complex on its distal surface; pli caballin appears to be complex (more than single), hypoglyph is deeply incised, but not so deep as to encircle the hypocone; protocone is rather small, rounded with a very long mesiobuccal pli that connects to the protoloph. The dP3and4 are large and "blocky" with parastyle and mesostyle as in dP2; pli caballins are obscured by matrix but appear to be single; hypoglyph of dP3 is as in dP2, but dP4 has a shallower hypoglyph; protocone is elongate and has a subtriangular shape in dP3 and is longer and more buccolingually compressed in dP4. The M1 is insufficiently erupted to expose details other than the mesio-distally narrow parastyle and the elongate triangular shaped protocone not yet fully in wear.

Morphology of the preorbital bar, lacrimal position and size and shallow depth of the preorbital fossa is similar to a number of taxa including "*Cormohipparion*" *africanum* (Bernor & White 2009), *Sivalhippus perimensis* (Wolf et al. 2013) and *Sivalhippus turkanensis* (Bernor & Harris 2003 and Bernor et al. 2010; sensu Wolf et al. 2013 in terms of generic identification)

### Bivariate Plots

Herein, we calculate a number of bivariate plots to compare length versus width occlusal dimensions of dP2-4 (M1 versus M3) and protocone length versus width (M10 versus M11) of the Olduvai specimen described herein and a sample of Eurasian and African hipparions following Wolf & Bernor (2013). Besides teeth from North American localities we analyzed specimens from various *Hippotherium* localities (Eppelsheim, Dorn-Dürkheim, and, for occlusal length-occlusal width plots, Höwenegg in Germany, Gols in Austria, localities potentially yielding two species of *Hippotherium* in Hungary as well as material from Baccinello, Italy; e.g., Bernor et al. 1997; Bernor & Franzen 1997; Bernor et al. 2003; Kaiser et al. 2003; Scott et al. 2005a, b; Kaiser & Bernor 2006; Bernor et

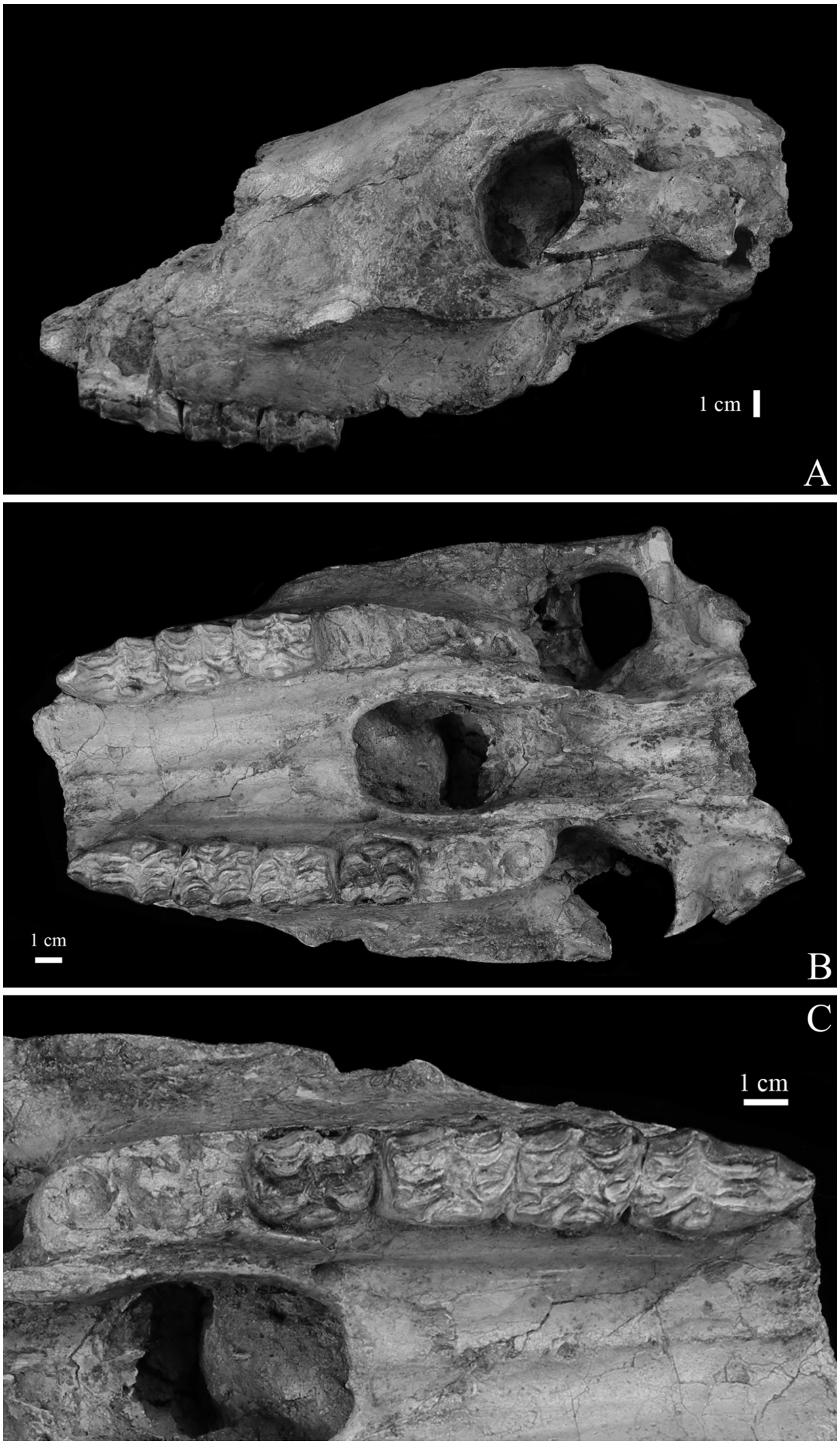


Fig. 1 - Olduvai skull RMNH67-5665. A) Lateral View, left side. B) Ventral View. C) Occlusal View, right side.

al. 2011; Wolf & Bernor 2013). The sample from Turkey includes a number of specimens belonging to separate hipparion lineages that were the product of a punctuated evolutionary event following the "Hipparion" Datum (Bernor et al. 2003). The Siwalik material represents a number of early members of the "*Sivalhippus*" Complex (Wolf et al. 2013), while the material from various Sub-Saharan African localities (*Eurygnathohippus*) and China can be referred to later members of the same complex (e.g., Bernor & Kaiser 2006; Bernor et al. 2010). Superspecific groups belonging to the "*Sivalhippus*" Complex include the genera *Sivalhippus, Eurygnathohippus, Plesiohipparion* and *Proboscidipparion* (Bernor & Lipscomb 1991; Bernor & Sun in press).

| Specimen Number | BONE | M1 | M3 | M5 | M6 | M7 | M8 | M9 | M10 | M11 |
|---|---|---|---|---|---|---|---|---|---|---|
| RMNH67/5665 | lt. dP2 | 41,5 | 21,8 | 13,3 | 1 |  |  | 1 | 8,6 | 4,1 |
| RMNH67/5665 | lt. dP3 | 29,1 | 21,3 | 16,1 | 1 | 4 | 1 | 2 | 8,9 | 3,6 |
| RMNH67/5665 | lt. dP4 | 28,0 | 21,6 | 15,4 | 3 |  |  | 0 | 10,1 | 3,1 |

**A**

| Specimen Number | BONE | M2 | M3 | M7 | M11 | M12 | M13 | M16 | M21 | M22 | M29 | M32 | M33 | M34 | M38 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| RMNH67/5665 | skull | 103,0 | 93,4 | 98,9 | 34,1 | 42,0 | 61,0 | 55,5 | 126,0 | 78,8 | 51,5 | 56,3 | 39,7 | 43,9 | 77,4 |

**B**

Tab. 1 - A) Measurements of *Eurygnathohippus cornelianus* RMNH67/5665, Olduvai Gorge, Tanzania deciduous cheek teeth: M1, occlusal length; M3, occlusal width; M5, mesostyle height; M6, number of plis on mesial border prefossette; M7, number of plis on distal border prefossette; M8, number of plis on mesial border postfossette; M9, number of plis on distal border postfossette; M10, protocone length; M11, protocone width. B) Measurements of *Eurygnathohippus cornelianus* RMNH67/5665, Olduvai Gorge, Tanzania skull: M2, palatal length; M3, vomerine length; M7, premolar length; M11, minimal breadth of choanae; M12, maximal breadth of the choanae; M13, palatal breadth between distal limit of P4s; M16, length of the fossa temporalis; M21, basioccipital breadth; M22, occipital height; M29, orbital diameter height; M32, distance between the orbit and the preorbital fossa (length of preorbital bar, or POB); M33, maximal length of the preorbital fossa (POF); M34, distance between the posterior limit of the preorbital fossa (POF) and the infraorbital foramen (IOF); M38, height of the posterior aspect of the POF above the alveolar border.

Sahabi, Libya (Bernor et al. 2008), Samos, Greece (Bernor et al. 1996a), and Maragheh in Iran (Bernor 1985, 1986, 1996b; Ataabadi et al. 2013) are important from the standpoint that they include lineage and species-diverse hipparion faunas. Not all localities are represented for all tooth positions and plotted measurements. All comparison data is taken from Bernor's equid database which to date includes over 16,000 measurement records.

### Occlusal length (M1) versus occlusal width (M3)

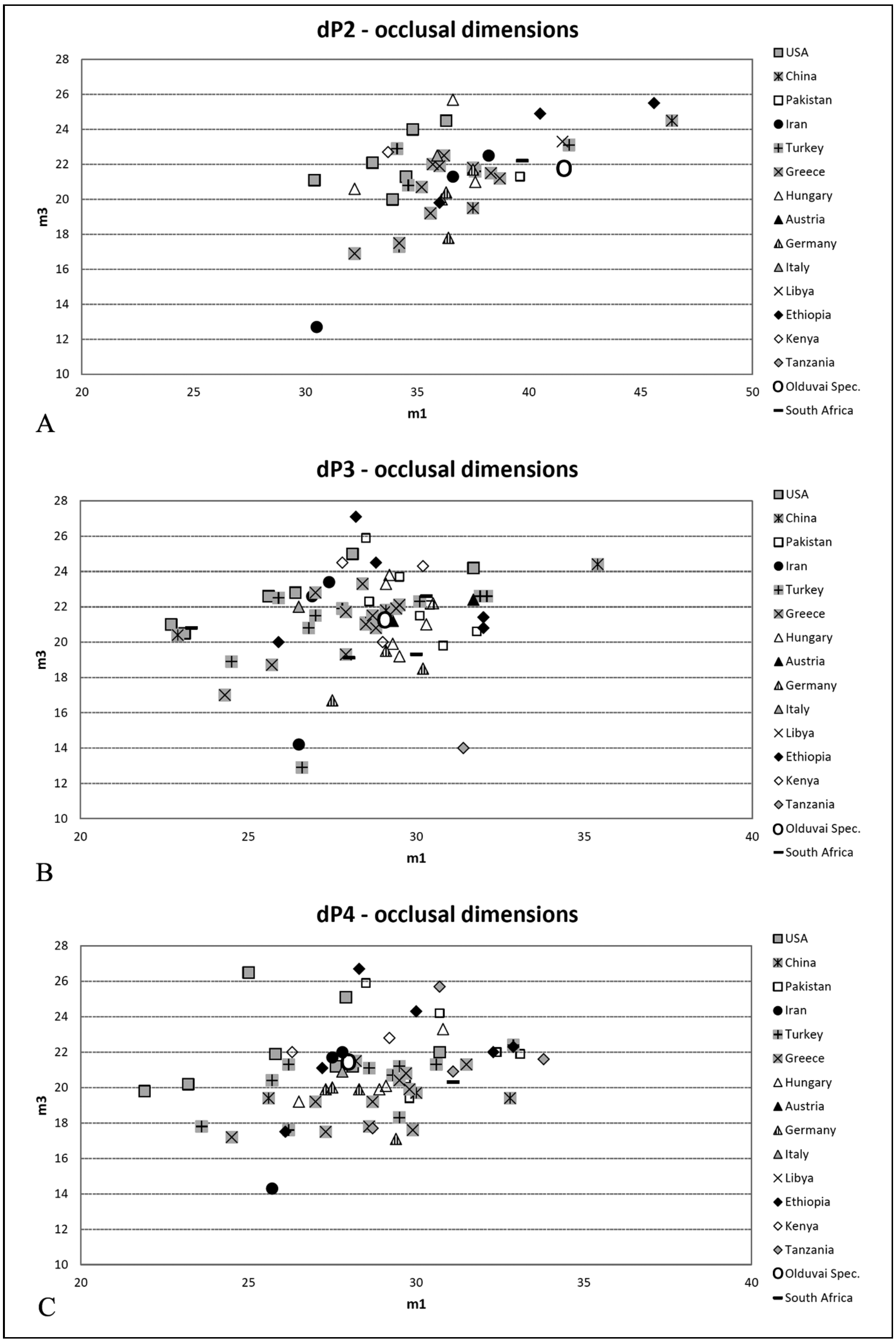
In order to characterize general size and basic occlusal proportions, we plot occlusal length (M1) versus occlusal width (M3) according to Bernor et al. (1997).

**dP2** (Fig. 2A): the dP2 of the Olduvai specimen described herein is among the largest (and especially longest) dP2s of our comparative sample. Only some other eastern African dP2s, a Libyan, a Chinese, and a Turkish specimen attain the same or a greater absolute length. All except for the Turkish tooth probably belonging to advanced members of the "*Sivalhippus*" Complex. Among these, the Olduvai specimen is particularly narrow or elongate. An additional Chinese dP2 and a few eastern African specimens as well as all teeth belonging to more basal members of the complex, such as the specimen from the Siwaliks and a *Eurygnathohippus hooijeri* specimen from Langebaanweg, South Africa, are slightly smaller. Teeth belonging to members of the *Hippotherium* clade (Dorn-Dürkheim, Höwenegg, Hungary, and Italy) plot consistently somewhat smaller than the Olduvai specimen. North American *Cormohipparion* mostly plots similar to Hungarian *Hippotherium*; these teeth are mostly somewhat wider in relative terms, or less elongate, than the remaining sample. In total, the Maragheh (Iran), Samos (Greece), and Turkish samples exhibit a considerable variation in size. One Maragheh dP2 is particularly small.

**dP3** (Fig. 2B): the plot of all dP3s compared herein exhibit a relatively dense cluster of data points, indicating a lower variation in absolute size and more consistent shape than seen in the dP2s. The Olduvai specimen is of average width and length and similar in size to Hungarian, Austrian, and Höwenegg *Hippotherium*; Dorn-Dürkheim and Italian specimens are somewhat smaller. North American *Cormohipparion* dP3s are of similar width, but have a great variation in length, while the presumably multispecific sample from Maragheh plots in two distinct positions, indicating somewhat shorter and much smaller teeth, respectively. Turkish and, to a lesser degree, Greek specimens show a considerable variation in length; the Turkish sample includes a very narrow dP3. Among the specimens from Samos, there is one cluster of data points plotting very close to the Olduvai specimen. Of the samples belonging to the "*Sivalhippus*" Complex, Siwalik as well as Ethiopian and Kenyan dP3s are similar in size to the Olduvai dP3, as are two of the three plotted *Eu. hooijeri* teeth from Langebaanweg, the third one being much shorter. An additional Tanzanian tooth is considerably narrower than the Olduvai specimen examined here. Chinese specimens are similar in width to the Olduvai specimen, but show remarkable variation in length.

**dP4** (Fig. 2C): dP4s in many ways plot similar to dP3s, but show a somewhat less clear concentration into one dominating cluster than seen in the dP3 length-width diagram; data points are more dispersed for measurement 1. It is noteworthy that all Siwalik and Langebaanweg specimens are longer than the Olduvai dP4, which suggests that they are from larger individuals,

Fig. 2 - Measurements of Occlusal Length (M1) versus Occlusal Width (M3). A) dP2. B) dP3. C) dP4.



possibly representing larger species. All additional Tanzanian specimens likewise plot to the right of the Olduvai specimen, only one being narrower. Also, Chinese specimens do not show length diversity as great as recorded for the dP3s. The Olduvai specimen plots close to the Italian tooth, but is somewhat shorter than the teeth forming the densest cluster of data points representing Samos.

### Protocone length (M10) versus protocone width (M11)

Dimensions of hipparion protocones provide additional useful systematic information. Our diagrams plot protocone length (M10) versus protocone width (M11).

**dP2** (Fig. 3A): protocones in dP2s are often difficult to measure especially when they are no longer isolated due to heavy wear (late wear stages). Nevertheless, the available data reveals some distinct patterns. The Olduvai dP2 protocone is amongst the longest ones of the comparison sample, but only of intermediate width. USA specimens (*Cormohipparion*) have a similar or smaller length, but are always wider in relative terms. *Hippotherium* protocones are consistently smaller, and in particular shorter than the Olduvai specimens. Langebaanweg protocones are shorter than the Olduvai

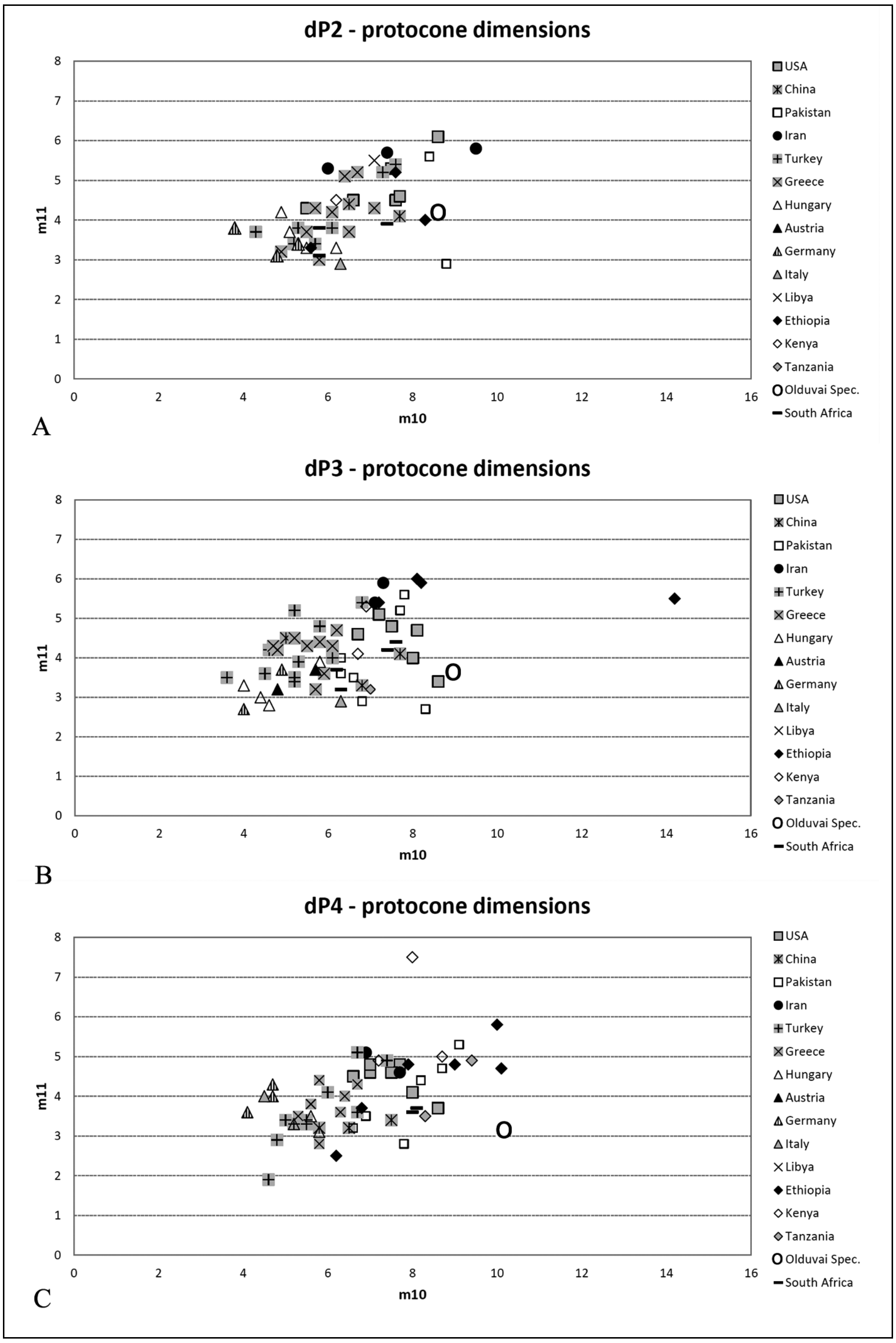


Fig. 3 - Measurements of Protocone Length (M10) versus Width (M11). A) dP2. B) dP3. C) dP4.

protocone, while the remaining Ethiopian and the Chinese data points plot similarly to the Olduvai protocone. Turkish specimens form two clusters: one with size dimensions similar to those seen in *Hippotherium* (Eppelsheim, Italy and Hungary), and one representing protocones that are of similar length but greater width than seen in the Olduvai specimen. The cluster indicating larger dimensions is in close proximity to the data points representing the lone Sahabi and the Maragheh specimens. Siwalik dP2 protocones have a length that is similar to the Olduvai protocones, but variable width. Greek hipparion protocones are smaller, but have a great size range due to the multiple lineages sampled.

**dP3** (Fig. 3B): protocone dimensions in dP3s plot in rather well confined cluster complexes for the individual localities considered here. The Olduvai dP3 protocone is narrow, but again among the longest of the comparison sample; only one of the remaining eastern African specimens has a protocone that is (considerably) longer. USA *Cormohipparion* specimens have protocones that are similar in size to the Olduvai protocone, but mostly wider. *Hippotherium* protocones are again consistently smaller than the Olduvai specimens (with the Italian specimen being comparatively narrow), as are the Turkish protocones. The latter ones form two weakly confined clusters here. Material from Samos has protocones that in this case plot closely together in between the two clusters of Turkish protocones. Langebaanweg and Chinese protocones are somewhat smaller than the Olduvai protocones, while the Maragheh data points indicate a length similar to those samples, but a greater width. Siwalik protocone dimensions form two distinct clusters here. Both clusters represent protocones that are somewhat shorter than the Olduvai protocone, but while the protocones of the first cluster have a width that is similar to the Olduvai protocones, the protocones of the second cluster are wider.

**dP4** (Fig. 3C): the clusters of data points representing dP4 protocone dimensions in the comparison material considered here, are similar in absolute and relative position to the clusters seen in the dP3 plot described above. The Olduvai dP4 protocone is among the most elongate specimens, showing a considerable length but a modest width. Eastern African protocones, while not reaching as great lengths as seen in the dP3s, often are among the longest specimens plotted here, but there are also some smaller protocones. This again results in substantial size variability in protocones from the Ethiopia, Kenya, and Tanzania sample. Dorn-Dürkheim *Hippotherium* dP4 protocones are noticeably wider than the Hungarian specimens, while the overall relative positions of the *Hippotherium* clusters with respect to the Olduvai specimens dimension is comparable to the condition seen in the dP3s. However, the Italian specimen plots much closer to the German material in the dP4 plot. Further differences between the plots for dP3 and dP4 protocones appear negligible.

## Summary

The bivariate plots of occlusal crown dimensions in dP2s reveal that the Olduvai juvenile skull is similar to other teeth belonging to advanced members of the "*Sivalhippus*" Complex in being larger and more elongate than most other Old and New World hipparion dP2s. In the plots representing the other deciduous cheek tooth positions, the Olduvai specimen is of only moderate size compared to the entire sample. The dP4 M1 versus M3 plot shows that many taxa have larger dimensions including samples of the "*Sivalhippus*" Complex from the Siwaliks, Africa, and China. There are also some large Turkish specimens as well as some material from Hungary and the USA; this is an indication of size of the species represented in our plots. Samples representing multispecific – multilineage localities such as China, Maragheh, Greece, and Turkey usually have a great range in size dimensions. The Olduvai *Eurygnathohippus cornelianus* dP2 is clearly derived and shares this relationship with other members of the "*Sivalhippus*" Complex.

Plots analyzing protocone dimensions in deciduous cheek teeth show more uniform dimensions across the individual tooth positions. The samples from various localities also appear to form more distinct clusters in the protocone plots than seen in the analysis showing overall width and length. We find that the protocones of the Olduvai material are consistently long, but relatively narrow. Other eastern African species protocones can have considerably greater dimensions. Protocones belonging to other, especially more basal, members of the "*Sivalhippus*" Complex, such as Siwalik and Langebaanweg hipparions, are somewhat smaller and compare in size to North American specimens' protocones. *Hippotherium* protocones (Gols, Dorn Dürkheim, Eppelsheim, Italy, and Hungary) are consistently smaller than "*Sivalhippus*" Complex protocones. Furthermore, *Hippotherium* data points plot in close proximity to some of the smaller Turkish protocones.

## Discussion

Bernor and Sun (in press) have discussed the morphology of Chinese *Plesiohipparion houfenense* and the constellation of characters that unite *Plesiohipparion* with *Eurygnathohippus*: maxillary cheek teeth with mesiodistally restricted "knife-like" parastyles and sometimes also mesostyles; protocones that are elongate, subtriangular shaped; metaconids and metastylids that are pointed lingually with accompanying broad and deep linguaflexids. Middle Awash, Olduvai and Omo Shungura F-K Plio-Pleistocene hipparions share these morphological features (Hooijer 1975: plates 14-17). These observations reinforce and augment previous assertions that the genus *Eurygnathohippus* is a member of the "*Sivalhippus*" Complex including at least the genera *Sivalhippus*, *Plesiohipparion*, *Eurygnathohippus* and also likely *Proboscidipparion* (Bernor & Lipscomb 1991; Wolf et al. 2013; Bernor and Sun, in press).

Our analyses herein further support the relationship between *Eurygnathohippus cornelianus* and the "*Sivalhippus*" Complex. A number of facial morphological features of the Olduvai juvenile skull described herein suggest that *Eu. cornelianus* has an ancestry related to early members of the "*Sivalhippus*" Complex. Included in this evolutionary relationship are Siwalik *Sivalhippus* species *S. nagriensis* and *S. perimensis* (late Miocene of the Siwaliks, ca. 10.6-8.0 Ma; Wolf et al. 2013), Lothagam Lower Nawata *Sivalhippus turkanensis* (Bernor & Harris 2003; Wolf et al. 2013) and Chinese *Plesiohipparion houfenense* (late Miocene-Pliocene of China, ca. 6-4 Ma; Qiu et al. 1987; Bernor & Sun, in press) which share the following characters: long preobital bar (POB) with lacrimal usually less than ½ the distance from orbit to posterior rim of preorbital fossa (POF); POF reduced in size, dorsoventrally restricted, placed high on the face and with no posterior pocketing (this particularly like *Plesiohipparion*). The dP2 occlusal length versus occlusal width dimensions show that *Eu. cornelianus* was lengthened compared to most hipparions except for members of the *"Sivalhippus"* Complex; however, *Eu. cornelianus* is not nearly so derived in this manner as Chinese *Proboscidipparion sinense.* Protocone length versus width likewise exhibits relationships to North American *Cormohipparion* as well as Chinese *Plesiohipparion*. The more primitive species *"Cormohipparion" africanum* from the early late Miocene of Bou Hanifia, Algeria (MN9, ca. 10.5 Ma), represents a very plausible sister taxon to the *"Sivalhippus"* Complex clade (Bernor & White 2009).

## Conclusions

Our study of Olduvai juvenile skull RMNH67/5665 referred to *Eurygnathohippus cornelianus* confirms its inclusion within the *"Sivalhippus"* Complex. Both morphological features of the face, morphology and dimensions of the deciduous cheek teeth support the conclusion that *Eurygnathohippus* likely diverged in the late Miocene from a taxon that was a primitive member of the *"Sivalhippus"* Complex clade. Recent work by Bernor and Sun (in press) based on a number of sectioned teeth of Chinese *Plesiohipparion houfenense, Proboscidipparion pater* and *Proboscidipparion sinense* suggest close phylogenetic relationships between *Plesiohipparion* and *Eurygnathohippus*. New, yet to be described material emerging from the late Miocene from Ethiopia, Kenya, and China will likely clarify these relationships further.

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