

## PHYLOGENETIC SIGNATURES IN THE JUVENILE SKULLS AND CHEEK TEETH OF PLEISTOCENE *PROBOSCIDIPPARION SINENSE*, CHINA

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**Abstract.** We describe and compare three partial skulls of Chinese juvenile *Proboscidipparion sinense* from the Nihewanian of China. Study of the facial morphology, especially the nasal aperture, as well as cheek tooth morphology and metric data, including length versus width of the maxillary cheek teeth of dP2, 3 and 4, support the conclusion that these skulls are referable to *Proboscidipparion sinense*. We reaffirm that *Proboscidipparion sinense* is a member of the “*Sivalhippus*” Complex that includes the following superspecific clades: *Sivalhippus*, *Eurygnathohippus*, *Plesiobhipparion* and *Proboscidipparion*. Recent studies by Bernor and Sun (2015) suggest that *Proboscidipparion* is particularly closely related to Chinese *Plesiobhipparion*, and more distantly related to *Eurygnathohippus* (exclusively Africa) and *Sivalhippus* (mostly South Asia).

### Introduction

Sefve (1927) produced the first detailed description of the extensive Chinese hipparionine horse collection maintained by the Palaeontologiska Museet, Uppsala, Sweden (PMU). He described 44 skulls, some associated with lower jaws, and a number of isolated jaws and limb bones. Most of this collection was from Baode, while others were from the Wuxiang, Yushe and Qingyang areas of China (Bernor et al. 1990, Fig. 1). Sefve (1927) described 11 species in the Uppsala collection, but nominated no type specimens, made no species diagnoses and paid little or no attention to these species ontogenetic variation (especially of the cheek teeth), and ignored the assemblage’s chronologic age.

Bernor et al. (1990) undertook a morphologic analysis of 40 discrete variables along with a metric

analysis on standardized measurements of hipparionine skulls, mandibles, teeth and bones following Eisenmann et al. (1988). As Sefve did not recognize any type specimens, Bernor et al. (1990) assigned Lectotypes for the Uppsala assemblage, including “*Hipparion*” *platyodus*, “*Hipparion*” *coelophyes*, “*Hipparion*” *hippidiodus*, “*Hipparion*” *ptychodus*, “*Hipparion*” *dermatorhinum*, “*Hipparion*” *forstenae*. Bernor et al. (1990) recognized PMU M3925 as the type specimen of the highly derived enigmatic species *Proboscidipparion sinense*. PMU M3925 was collected from Locality 39, Langou, Mianchi County, Henan Province, China (Zdansky 1923). *Proboscidipparion sinense* is also known from the early Pleistocene (ca. 2.0 Ma) Nihewan, Yangyuan, Hebei Province Yushe Basin, Shanxi Province, Kehe, Shanxi Province (the latest *Proboscidipparion* in China, ca. 1 Ma), Heshui, Gansu Province (Qiu et al. 1987), Longdan, Gansu Province (Qiu et al. 2004) and Tangshan, Nanjing, Jiangsu Province (Dong & Fang 2005). While the more primitive form, *Proboscidipparion pater* is known from the early Pliocene of Yushe Basin, Shanxi Province (Qiu et al. 1987), Linxia Basin, Gansu Province (Deng et al. 2014) and Xihe, Gansu Province (Wang et al. 2014). Recently, Deng (2012) has reported a skull of *Proboscidipparion sinense* from the basal Quaternary (ca. 2.6 Ma) locality of Longdon, Dongxiang County, Gansu Province that significantly supplements our understanding of the cranial and dental anatomy of this species and suggests its possible relationship with a Chinese Miocene hipparion species, *Hipparion dermatorhinum* (Deng, 2012).

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Qiu et al. (1987) undertook a major review of Chinese hipparions. The authors recognized *Proboscidipparion* as a subgenus of *Hipparion*, *Hipparion* (*Proboscidipparion*) with two species: *H. (P.) pater* and *H. (P.) sinense*. Qiu et al. (2004), Dong and Fang (2005), Deng (2012), Sun (2013) and (Wang et al. 2014) followed this nomenclatural convention. Qiu et al. (1987) reported the stratigraphic range of the genus *Proboscidipparion* (his subgenus *Hipparion* (*Proboscidipparion*)) in China as being Gaozhuangian to early Zhoukoudianian (ca. 5-1 Ma). Bernor et al. (1990, 2010) have recognized the relationship between *Proboscidipparion*, Siwaliks hipparions (*Sivalhippus* spp.) and Africa hipparions (*Eurygnathohippus* spp.). Zouhri and Bensalmia (2005) identified *Proboscidipparion* as a genus that includes three subgenera: *Proboscidipparion*, *Plesiohipparion* and *Eurygnathohippus*. Bernor and Sun (2015) recognized *Proboscidipparion* as a valid genus and provided evidence of its inclusion within the “*Sivalhippus*” Complex that includes the genera *Sivalhippus*, *Proboscidipparion*, *Plesiohipparion* and *Eurygnathohippus*.

This contribution continues work undertaken by Wolf and Bernor (2013) and Bernor et al. (2014) to study the morphology and phylogenetic signaling of hipparionine juvenile skulls, jaws and cheek teeth. Of all known hipparions, *Proboscidipparion* is one of the most derived, particularly in its very elongate, curved snout and highly retracted nasals believed to have supported a tapir-like mobile snout (Qiu et al. 1987). Until now, it has been assumed that *Proboscidipparion* was autochthonous to China. However, as suggested by Bernor and Sun (2015), its range may have extended westward into Western Eurasia. This possibility is under study by Bernor and Sen (in prep.)

## Materials, Methods and Abbreviations

The juvenile skulls are housed by the American Museum of Natural History (F: AM numbers) and the Tianjin Museum of Natural History, Tianjin, China (THP number).

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) 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 *Proboscidipparion sinense* juvenile skulls considered herein, and a large data set following Wolf and Bernor (2013) and Bernor et al. (2014). We use SYSTAT 12.0 to calculate plots. The Eppelsheim sample of adult P2, P3 and P4 is used to calculate 95% confidence ellipses because of the large sample size of a single primitive Old World hipparion species, *Hippotherium primigenium* (re: Bernor et al. 1997).

The localities used for comparison to China *Proboscidipparion sinense* (indicated by upper case C) include:

a – North American *Cormohipparion occidentale* from the American Museum of Natural History Frick Collection, New York (AMNH) (Bernor et al. 1996; Woodburne 2007).

b – Sahabi, Libya (late Miocene) collection maintained by the Institute for Science and Medicine (ICSM), Martinsville, Virginia (Bernor et al. 1987; Bernor & Scott 2003; Bernor et al. 2008; Bernor et al. 2012).

c – China (early Pleistocene) lower case c is for non-*Proboscidipparion sinense* Chinese specimens derived from the AMNH, Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing and Tianjin Museum of Natural History, Tianjin (THP) (Bernor et al. 1990; Bernor & Lipscomb 1991; 1995; Bernor & Sun 2015).

e – Ethiopia (late Miocene-Pleistocene) *Eurygnathohippus* spp. maintained by the National Museum of Natural History, Addis Ababa (Bernor et al. 2005; Gilbert & Bernor 2008; Bernor & Haile-Selassie 2009; White et al. 2009; Bernor et al. 2013; Melcher et al. 2014).

g – Germany (late Miocene) *Hippotherium primigenium* maintained by the Senckenberg Museum, Frankfurt and the Hessisches Landesmuseum, Darmstadt (Bernor et al. 1996, 1997; Bernor & Franzen 1997; Kaiser et al. 2003; Wolf & Bernor 2013).

h – Hungary (Late Miocene) *Hippotherium primigenium* and related species *Hippotherium intrans*, *Hippotherium sumegense*, *Hippotherium microdon*, *Hippotherium csarkevareense* maintained by the Geological Institute of Hungary, Budapest (Bernor et al. 1996; Bernor et al. 1999; Bernor et al. 2003a; Scott et al. 2005a and b; Kaiser & Bernor 2006)

k – Kenya (Late Miocene-Pleistocene) *Eurygnathohippus* spp. maintained by the Kenya Museums of Natural History, Nairobi (Hooijer 1975; Bernor & Harris 2003; Bernor 2007; Bernor et al. 2010)

l – Langebaanweg, South Africa (early Pliocene) *Eurygnathohippus hooijeri* maintained by the Natural History Museum of Cape-town (Bernor & Kaiser 2006).

n – Sinap, Turkey (late Miocene) *Cormohipparion* and “*Hipparion*” spp. maintained by the Natural History Museum of Ankara (Bernor et al. 2003b).

p – Pakistan, Siwalik collection (late Miocene) of the Yale-Geological Survey of Pakistan (YGSP) survey currently maintained by the Laboratory of Evolutionary Biology, Howard University (Wolf et al. 2013).

s – Samos, Greece (Late Miocene) collection of *Cremohipparion*, *Hipparion* s.s. and *Hippotherium* maintained by the AMNH, New York (Bernor & Tobien 1989; Bernor et al. 1996).

t – Tanzania (late Miocene) collection of *Eurygnathohippus* spp. maintained by the Natural History Museum of London (BMNH) and Natural History Museum of Tanzania, Dar es Salaam (Leakey 1965; Bernor & Armour-Chelu 1999; Armour-Chelu et al. 2006; Wolf et al. 2010; Armour-Chelu & Bernor 2011; Bernor et al. 2014).

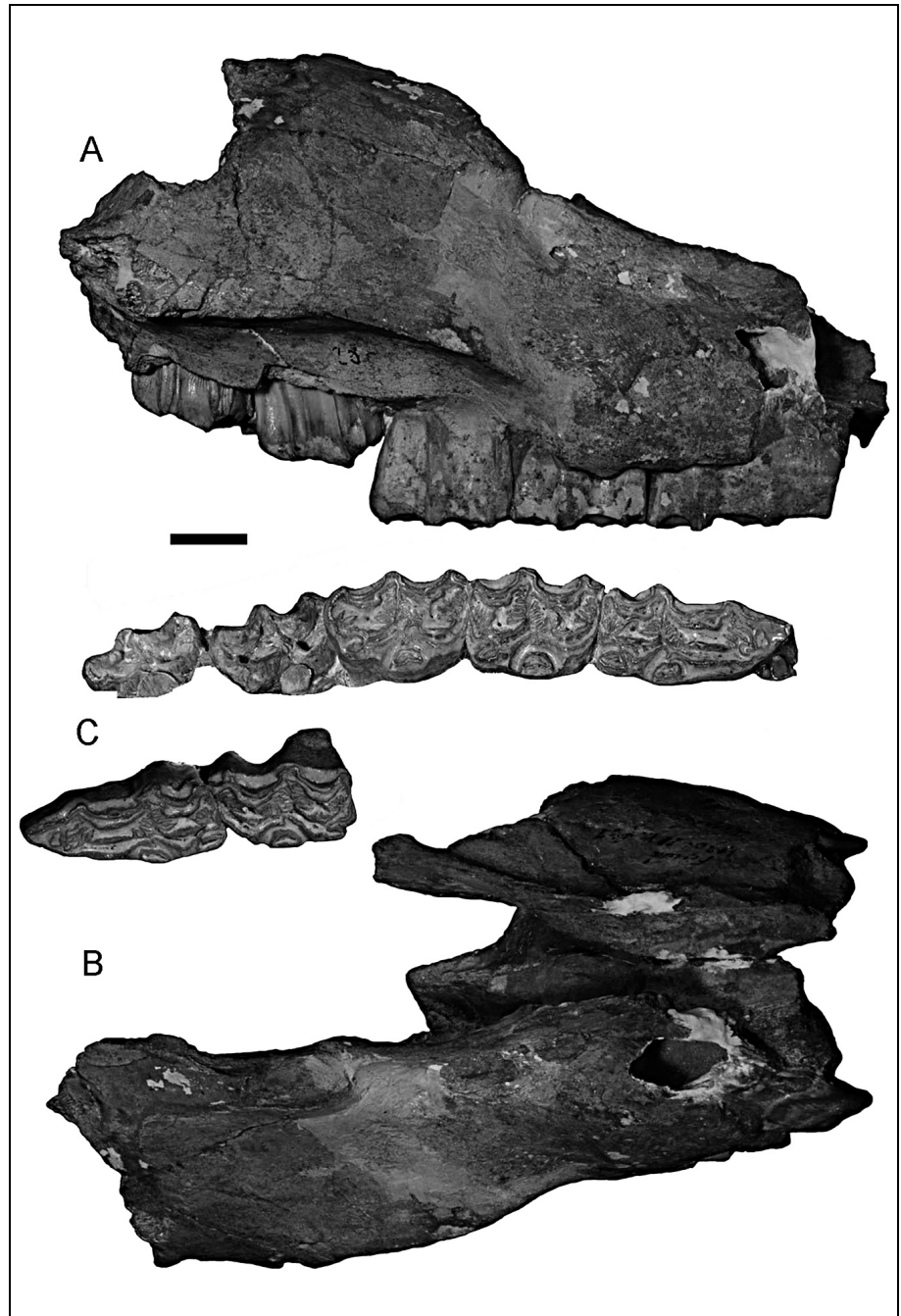
v – Vienna Basin (late Miocene) collection of *Hippotherium primigenium* maintained by the Natural History Museum of Vienna (Bernor et al. 1988; Bernor et al. 1996; Scott et al. 2005a and b).

Z – Calta, Turkey (early Pliocene) “*Hipparion*” *heintzi* maintained by the Museum National d’Histoire Naturelle, Paris (Eisenmann & Sondaar 1998)

## 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 and 2011) updated these conventions in terms of anatomical and systematic nomenclature that we follow herein. Our use of

Fig. 1 - Juvenile skull fragment THP00149. A) Lateral view; B) oblique fronto-dorsal view; C) occlusal view. Scale bar here and for all figures 1-3 = 2 cm



a comprehensive data set for Old World hipparionine deciduous teeth follows the detailed initial analysis by Wolf and Bernor (2013). Recognition of the validity of the African hipparion genus *Eurygnathohippus* (van Hoepen, 1930) follows observations and analyses by Bernor and Armour-Chelu (1999); Bernor and Harris (2003), Armour-Chelu et al. (2006); Bernor et al. (2005) Bernor and Kaiser (2006), Bernor (2007); Bernor et al. (2008); Gilbert and Bernor (2008); Bernor and Haile-Selassie (2009); Bernor and White (2009); Bernor et al. (2010); Wolf et al. (2010); Armour-Chelu and Bernor (2011); Bernor et al. (2012); Melcher et al. (2014); Bernor et al. (2013); Bernor and Sun (2015).

#### Morphological Observations and Comparisons - Description of Juvenile Skulls THP00149, F: AM11736 and F: AM125709

There are three juvenile skulls of *Proboscideipparion sinense* that we analyse here: THP00149 (Fig. 1A-C), F: AM11736 (Fig. 2A-C) and F: AM125709 (Fig. 3A-C). Measurements on the cheek teeth of these three specimens are given in Tab. 1.

THP00149 (Fig. 1A-C) is a juvenile palate with dP2-4 and M1 and M2 emerging from their crypts. It is derived from the type Nihewan fauna, China. The lateral aspect (Fig. 1A) exhibits no preorbital fossa (POF)

Specimen Number	Species	Mammal Age	Element	Age (Ma)	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11
THP00149	<i>Proboscoidipparion sinense</i>	Nihowan	txdP2	2.0	50.2		24.7			3	7	6	5	6.4	4.3
			txdP3	2.0	33.0		25.9			7	9	7	6	7.7	4.0
			txdP4	2.0	36.3		24.4			11	9	7	2	7.6	4.0
F:AM117336	<i>Proboscoidipparion sinense</i>	Nihowan	txdP2	2.0	37.5		19.5		25.5	3	2	3	0	6.5	4.4
			txdP3	2.0	29.1		21.8		17.2	2	5	3	1	6.8	3.3
			txdP4	2.0	30.0		19.7			2	5	3	0	5.8	3.2
F:AM125709	<i>Proboscoidipparion sinense</i>	Nihowan	txdP2	2.0	46.4		24.5		20.4	2	2	2	0	7.7	4.1
			txdP3	2.0	35.4		24.4		16.6	3	6	4	2	7.7	4.1
			txdP4	2.0	32.8		19.4		14.5	3	3	2	0	7.5	3.4

Tab. 1 - Measurements of three maxillary dentitions of juvenile *Proboscoidipparion sinense* (THP00149, F: AM117336; F:AM125709): 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.

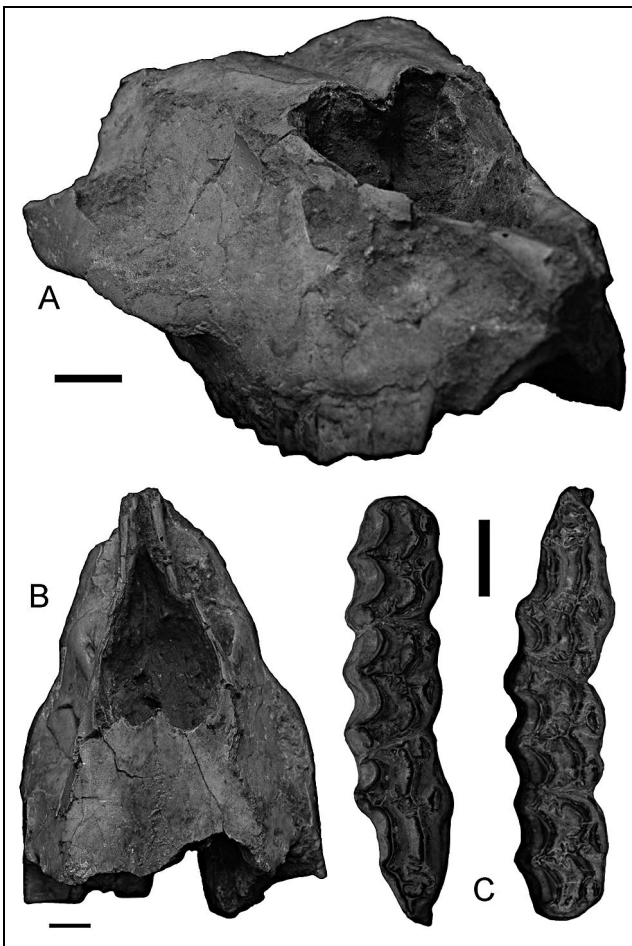


Fig. 2 - Juvenile skull fragment F:AM117336. A) Oblique-frontal view; B) dorsal view; C) occlusal view.

and there are no nasal bones projecting anteriorly. The dorso-oblique frontal view (Fig. 1B) exhibits a nasal aperture that is restricted rostrally and broadens greatly distally above the dP4 mesostyle. There is no evidence of nasal bones dorsally leaving a very extensive, open

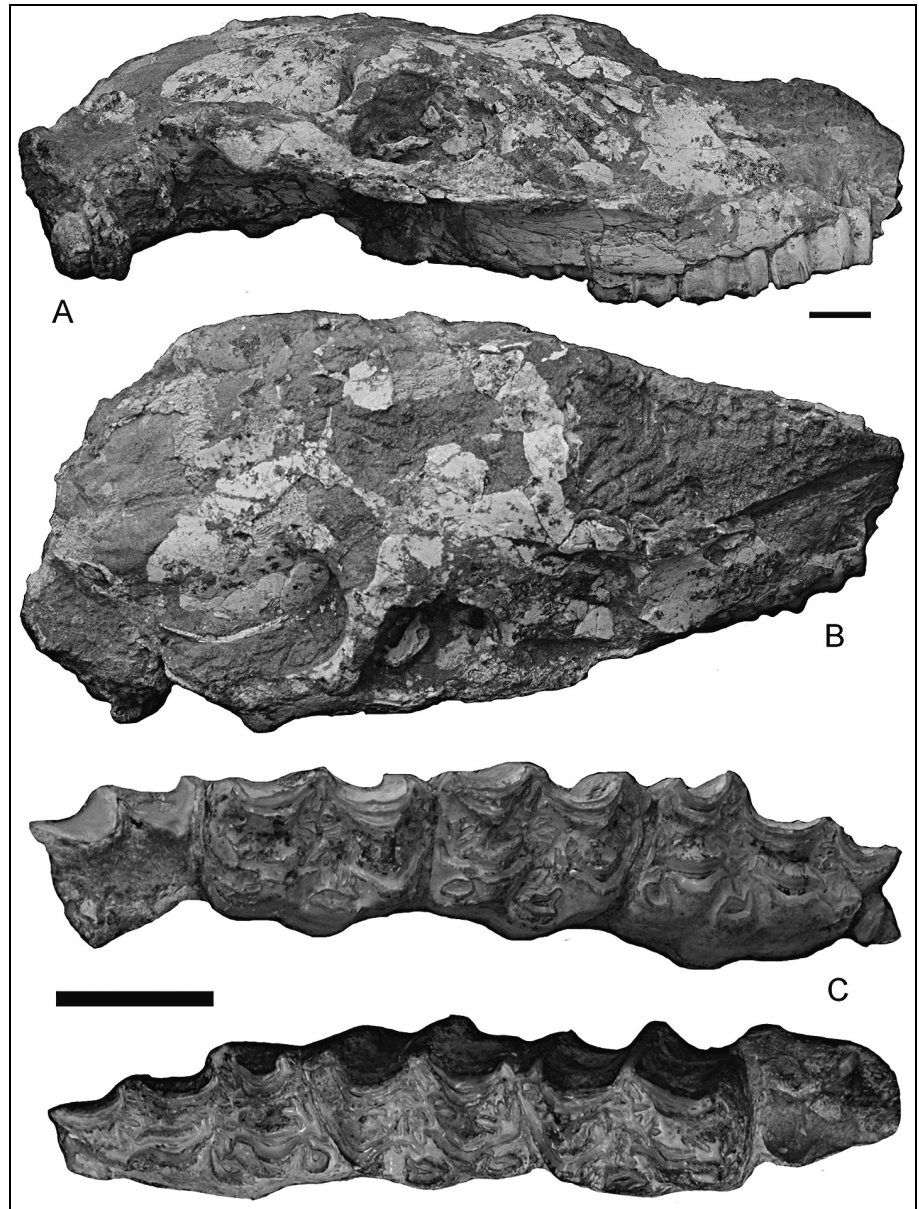
aperture. The occlusal view (Fig. 1C) exhibits the following salient features: dP2 is very long, especially the portion mesial to the mesostyle; plication frequency is very high on dP2 and dP3 fossettes, less so due to earlier wear on dP4; pli caballins are single; protocones are lingually flattened, labially rounded and not lengthened on all dPs. All dPs are large. M1 and M2 are unworn.

F: AM125709 (BX bh B825, China 1936; Fig. 2A-C) is very similar to THP00149 in its morphological details. It is derived from S.E. Shansi, Hsin Chuang, 13 miles south of Shou Yang Town. There is no preorbital fossa (Fig. 2A). The nasal aperture is restricted rostrally, very broad and open distally where they extend to dP4 mesostyle (Fig. 2B). The dP2 is very elongate, especially anterior to the mesostyle. While the protocones are somewhat larger and not lingually flattened, the other occlusal features are as in THP00149 (Fig. 2C)

F: AM117336 (China 64-8759 Hsia Kou, 3 mi. NW of Yushe Town, List-3, S.E. Shansi, 1936; Fig. 3A-C) is similar to the other two specimens in features of the face and nasal aperture. The lateral view of this specimen (Fig. 3A) clearly demonstrates that there is no preorbital fossa and the nasals are retracted at this ontologic stage to above emerging right M1. The antero-oblique view (Fig. 3B) very clearly demonstrates the strong retraction of the nasals and the broad, lateral opening most distally, characteristic of juvenile *Proboscoidipparion sinense*. The cheek teeth are somewhat smaller, dP2 is shorter but other occlusal features are particularly similar to F: AM125709 (Fig. 3C). This specimen is also smaller, overall than the other two specimens.

These three specimens are consistent in the following salient features characteristic of *Proboscoidipparion sinense*: facial region lacks any remnant POF; nasals are strongly retracted and open dorsally to the mesos-

Fig. 3 - Juvenile skull fragment F:AM125709. A) Lateral view; b) oblique fronto-dorsal view; c) occlusal view.



tyle of dP4 with no evidence of a projecting dorsally placed nasal bone; dP2s are very elongate; deciduous cheek teeth with complex pre- and postfossettes, small protocones often lingually flattened and labially rounded. These characters agree well with adult cheek teeth of *Proboscidipparion* except dP2 is longer than P2 (Bernor & Sun 2015).

#### 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 three specimens of juvenile *Proboscidipparion sinense* described above following Wolf and Bernor (2013) and Bernor et al. (2014). In each plot we calculate a 95% confidence el-

lipse for Eppelsheim P2, P3, and P4 (permanent teeth): length (M1) versus width (M3) (Figure 4A-C) and protocone length (M10) versus width (M11) (Figure 5A-C) of Eurasian and African hipparions dP2s, dP3s and dP4s cited above in the Abbreviations section. There are insufficient Eppelsheim dP2s-4s to calculate 95% confidence ellipses, hence the use of the adult P2-4s for these comparisons.

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

dP2 (Figure 4A). Eppelsheim P2 is plotted with faint circles indicating individual bivariate points for that locality's specimens. Frequently, dP2s are mesiodistally longer than corresponding P2s in adults of the same species. This plot shows that 3 late Miocene specimens of *Cormohipparion* from the United States (a) plot within the ellipse along with a specimen of *Cormohip-*

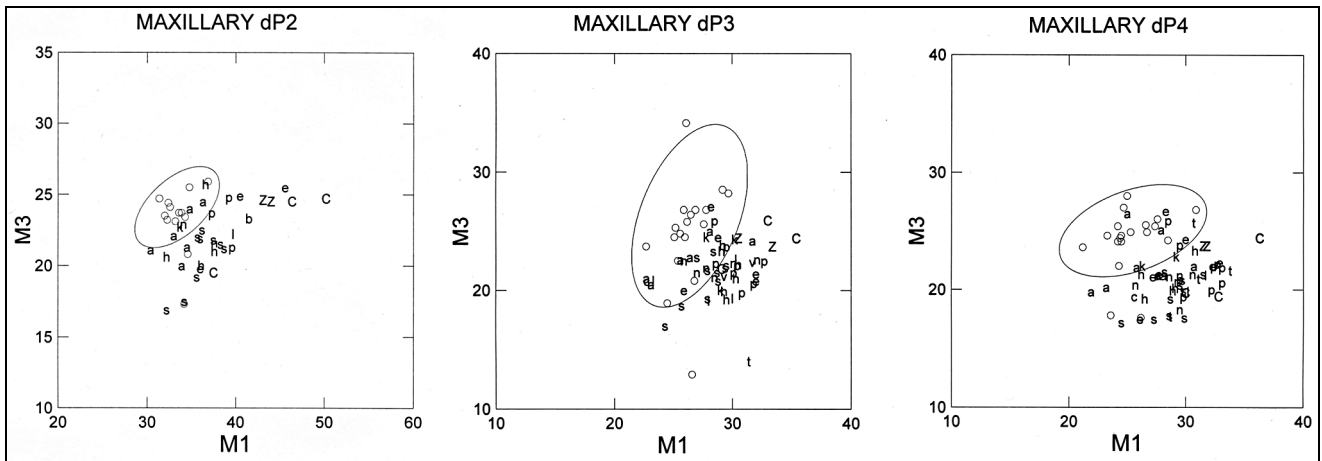


Fig. 4 - Bivariate Plots of dP2-4, occlusal length (M1) versus occlusal width (M3), 95% confidence ellipse from the Eppelsheim, Germany (10.3 Ma) sample of dP2-4: A) dP2; B) dP3; C) dP4. Localities as referenced in the Materials, Methods and Abbreviation section.

*parion sinapensis* from Sinap (n) and a specimen of *Eurygnathohippus feibeli* from Kenya (k). There are specimens from North America (a = *Cormohipparion*), Hungary (h = *Hippotherium*) Pakistan (p = *Sivalhippus* and “*Hipparion*” sp.), and Samos (s = *Hipparion* spp. and *Cremohipparion* spp.) to the right and below the ellipse. Wider and longer dP2s are known of *Eurygnathohippus hasumense* from Ethiopia (e), “*Hipparion*” sp. from Sahabi (b), “*Hipparion*” *heintzi* from Calta (Z). The longest dP2s are of Nihowan *Proboscoidipparion sinense* (C; F: AM125709 and THP00149); F: AM117336 is shorter and narrower). The longer and longest (M1) specimens are all members of the “*Sivalhippus* Complex”; lengthened dP2s are a synapomorphy of this superspecific clade.

**dP3** (Figure 4B). The Eppelsheim P3 95% confidence ellipse is larger in its dimensions due to great ontogenetic variation for width (M3). Crowded within the lower right quadrant of the ellipse are a number of North American (a) *Cormohipparion occidentale* specimens, Samos (s) *Cremohipparion* and *Hipparion*, Sinap (n) “*Hipparion*” and Pakistan (p) *Sivalhippus nagriensis*. There are a large number of plotted specimens just to the lower right and outside the lower right portion of the ellipse from North America (a), Sinap (n) and Pakistan (p) of these same taxa. Also outside the lower right margin of the ellipse are Vienna Basin *Hippotherium primigenium* (v), Samos (s) hipparions, Langebaanweg *Eurygnathohippus hooijeri* (l), Pakistan *Sivalhippus* (p) and Ethiopia *Eurygnathohippus* (e). The widest (M3) specimens to the right of the ellipse are of Calta “*Hipparion*” *heintzi* (Z), China *Proboscoidipparion sinense* (C) and a specimen of North American *Cormohipparion* (a). The narrowest dP3 (M3) is from Laetoli, Tanzania (t) *Eurygnathohippus* sp.

**dP4** (Figure 4C). The Eppelsheim P4 95% confidence ellipse is smaller than the one for P3 and therefore the variability in Eppelsheim dimensions are less for this

tooth than P3. Plotted within the ellipse are specimens of North American (a) *Cormohipparion*, Pakistan (p) *Sivalhippus nagriensis*, Ethiopian (e) *Eurygnathohippus hasumense* and Tanzania (t) *Eurygnathohippus* sp. The majority of the plotted specimens are from below the Eppelsheim ellipse including specimens from North America (a) *Cormohipparion*, Sinap (n) “*Hipparion*” spp., Hungarian (h) *Hippotherium* spp., Samos (s) *Cremohipparion* spp. and *Hipparion* spp., Langebaanweg (l) *Eurygnathohippus hooijeri* and Tanzanian (t) *Eurygnathohippus*. The smallest (specifically in width, M3) specimens are from Samos (s) and Ethiopia (e) *Cremohipparion* and *Eurygnathohippus*, respectively. Calta (Z) “*Hipparion*” *heintzi* has two large (length and width) dP4s located just to the right of the Eppelsheim ellipse. The longest dP4 is of China (C) *Proboscoidipparion sinense* THP00149; the other 2 specimens of *Proboscoidipparion sinense* (C) are smaller both in length and width. DP4 does not as conclusively segregate *Proboscoidipparion sinense* from other taxa as does dP2, but it does include an individual with the longest dP4.

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

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

**dP2** (Fig. 5A). The Eppelsheim P2 95% confidence ellipse for protocone length (M10) versus protocone width (M11) include most of the plotted dP2 M10 versus M11 specimens within it, including specimens from China (C), Calta (Z), North America (a), Sinap (n), Samos (s), Sahabi (b), Ethiopia (e), Kenya (k) and Langebaanweg (l). The widest protocone is of “*Hipparion*” *heintzi* (Z) from Calta plotted just outside the top of the ellipse, where the narrowest protocones are of *Sivalhippus nagriensis* are from Pakistan (p) which plot

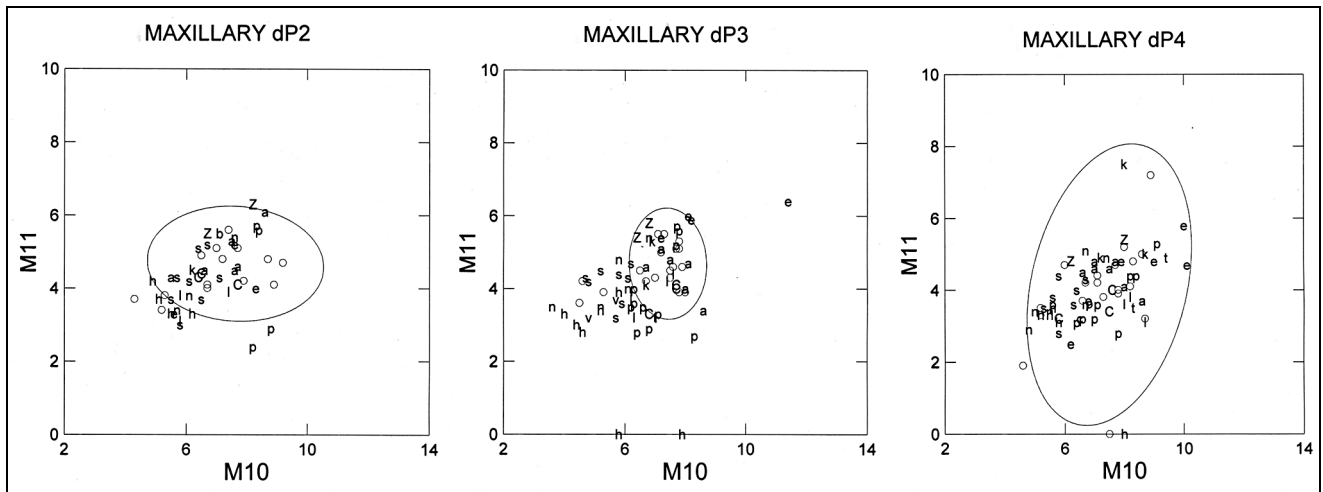


Fig. 5 - Bivariate Plots of dP2-4, protocone length (M10) versus protocone width (M11), 95% confidence ellipse from the Eppelsheim, Germany (10.3 Ma) sample of dP2-4: A) dP2; B) dP3; C) dP4. Localities as referenced in the Materials, Methods and Abbreviation section.

outside the lower border of the ellipse. The longest protocones include specimens of Eppelsheim *Hippotherium primigenium*, North American *Cormohipparion* (a), Pakistan *Sivalhippus* (p) Ethiopian *Eurygnathohippus* (e), Chinese *Proboscidiiparion* (C) and Calta “*Hipparion*” *heintzi* (Z). Long protocones are diagnostic for *Cormohipparion* and members of the *Sivalhippus* Complex (Wolf et al. 2013; Bernor & Sun 2015) and are primitive for Old World hipparionines.

*dP3* (Fig. 5B). The Eppelsheim P3 95% confidence ellipse for protocone length (M10) versus protocone width (M11) exhibits less variability than for dP2; hence the smaller ellipse. Included within this ellipse are specimens of species previously cited from North America (a), Sinap (n), Calta (Z), Samos (s, with only two specimens just inside the left border of the ellipse), Ethiopia (e), Kenya (k), Langabaaanweg (l) and North America (a). Specimens to the left of the ellipse are derived from Samos (s), Sinap (n), the Vienna Basin (v), Hungary (h) and Pakistan (p). The narrowest protocones are from Hungarian *Hippotherium* (h) and Pakistan *Sivalhippus nagriensis* (p). The largest protocone, both in length and width is of Ethiopian *Eurygnathohippus hasumense* (e).

*dP4* (Fig. 5C). The Eppelsheim P4 95% confidence ellipse for protocone length (M10) versus protocone width (M11) exhibits a very large range of variation with all of the comparative sample contained within the Eppelsheim P4 95% confidence ellipse. The widest protocone is of Kenyan *Eurygnathohippus* (k). The longest protocones are of Ethiopian *Eurygnathohippus* (e). *Proboscidiiparion sinense* (C) protocones plot in the lower center portion of the ellipse, with “*Hipparion*” *heintzi* specimens being marginally wider.

## Summary

Wolf, Bernor (2013), Bernor et al. (2014), Bernor and Sun (2015) have recently discussed hipparion cheek tooth morphology. In this study, we reaffirm a number of their observations. First, members of the “*Sivalhippus*” Complex generally have amongst the longest dP2s and longest protocones. We show here that *Proboscidiiparion sinense* has, although somewhat variable, the longest dP2s of all hipparions that we have studied and this should be considered a shared-derived character of this clade. It is interesting that Calta “*Hipparion*” *heintzi* also has a very long dP2, and as such has possible affinities with *Proboscidiiparion*. This will be considered further in a manuscript being prepared by Bernor and Sen (in prep.). The longest protocones are found in *Cormohipparion* and members of the “*Sivalhippus*” Complex: *Sivalhippus*, *Eurygnathohippus*, *Plesiohipparion* and *Proboscidiiparion* (Bernor & Sun 2015). Bernor et al. (2011) have further noted that advanced members of Central European *Hippotherium* evolved short protocones later in the Turolian. These lines of evidence are revealed herein.

## Discussion

Bernor and Sun (2015) have discussed the morphology of Chinese *Plesiohipparion houfenense*, *Proboscidiiparion pater* and *Proboscidiiparion sinense* based on a series of 18 sectioned cheek teeth. They documented the morphologic changes through these sectioned cheek teeth’s ontogeny and discovered synapomorphies between these taxa and Eurasian and African lineages. Bernor and Sun (2015) confirmed that these Chinese hipparions shared numerous synapomorphies with European and West Asian *Plesiohipparion* and African *Eu-*

*rygnathohippus* spp. The characters shared between these last two taxa, *Plesiohipparion* and *Eurygnathohippus*, were particularly extensive, and together with *Proboscidipparion* were likely related to the Indopakistan *Sivalhippus* clade (sensu Wolf et al. 2013).

Adult *Proboscidipparion sinense* has an extremely elongate snout with the nasal bones retracted nearly to the anterior orbit (re: Bernor et al. 1990, Figs. 17A and 17B). There is no preorbital fossa. The incisor teeth are large, I3 is very long mesiodistally, all incisors have distinct grooves on their labial and lingual surfaces. There are no canines. The cheek teeth have extremely complex plications of the pre- and postfossettes, complex pli caballins, deeply incised hypoglyphs and triangular-shaped, elongate protocones with a flattened lingual aspect. The P2 anterostyle is elongate (Bernor et al. 1990, Fig. 17A & B). Bernor and Sun (2015) characterized *Proboscidipparion pater* middle stage-of-wear maxillary cheek teeth as having: knife-like pointed parastyle and metastyle; pre- and postfossettes are richly plicated; pli caballin is single; hypoglyph is moderately deeply incised. Bernor and Sun (2015) characterized *Proboscidipparion sinense* middle stage-of-wear maxillary cheek teeth as having: parastyle pointed and knife-like; mesostyle more rounded; prefossette complex on both mesial and distal borders, postfossette is more complex on its mesial border than distal border until late wear when all borders are complex, but with short plis; pli caballin varies from being double to triple; hypoglyph is very deeply incised in early wear becoming moderately deeply incised by middle stage-of-wear; protocone is elongate oval but becoming rounder in late wear.

In the three juvenile skulls we describe here, facial features and nasal retraction is very similar to the adult condition. Maxillary deciduous cheek teeth have: extremely elongate dP2 anterostyle; very complex plications

of the pre- and postfossettes; hypoglyphs very deep to surrounding hypocone; protocones markedly shorter than in the adults, but exhibiting lingual flattening as is common in members of the *Sivalhippus* Complex, and in particular Indopakistan species of *Sivalhippus* (Bernor & Hussain 1985 and Wolf et al. 2013).

## Conclusions

Juvenile skeletal material is most often ignored by the paleontological community. This has especially been the case in studying hipparions. We have found through recent publications (Wolf & Bernor 2013; Bernor et al. 2014; Bernor & Sun 2015) that “*Sivalhippus*” Complex taxa in particular provide phylogenetic signals in their skull, particularly facial, and maxillary cheek tooth morphology. In this contribution we show unique shared-derived characters of the genus *Proboscidipparion*: strongly reflected nasal bones with a very wide nasal aperture distally; lacking preorbital fossa; dP2s extremely elongate; maxillary cheek tooth pre- and postfossettes with highly complex plications. Thusfar, *Proboscidipparion* has only been reported as being endemic to China, but work recently undertaken by Bernor and Sen (in prep.) will investigate if this clade extended its range into Western Eurasia.

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