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SHANXIHIPPUS DERMATORHINUS COMB. NOV. WITH COMPARISONS TO OLD WORLD HIPPARIONS WITH SPECIALIZED NASAL APPARATI

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Keywords: *Shanxihippus dermatorhinus*; late Miocene; Phylogeny; Biogeography.

Abstract. Skulls, mandibles and dentitions of a new, monospecific lineage of late Miocene Chinese hipparionine horse, *Shanxihippus dermatorhinus* comb. nov are reported. We frame our description of this newly recognized genus with a comparison to primitive North American hipparion, *Cormohipparion occidentale* and Central European *Hippotherium primigenium* from the Vienna Basin and Hoewenegg, Germany. We recognize, for the first time that the Chinese early late Miocene hipparion "*Hipparion" weihoense* is primitive and referable to *Hippotherium* extending the range of that lineage in the early late Miocene (MN9 equivalent) from China to Central and Western Europe. We develop a multistate 53 character state analysis including primitive species of *Hippotherium, Sivalhippus, Shanxihippus, Cremohipparion* and *Proboscidipparion* to undertake a cladistic analysis using four consecutively further removed North American outgroups: *Cormohipparion occidentale, Cormohipparion quinni, Merychippus insignis* and *Parahippus leonensis*. We evaluate the phylogenetic relationships of these taxa and pose hypotheses of origin and biogeographic distribution of these superspecific taxa in the late Miocene of Eurasia. We conclude that *Shanxihippus, Cremohipparion* and *Proboscidipparion* are three distinct clades, held at Genus rank, that have converged in their snout lengthening and nasal retraction likely due to similarities in feeding adaptation.

Introduction

North American *Cormohipparion* extended its range into Eurasia and Africa between 11.4 and 11.0 Ma and represents the evolutionary source for the *Cormohipparion* (former *Hipparion*) Datum (Bernor et al. 2017). Old World *Cormohipparion* occurred in the Indian Subcontinent, Turkey and Africa. European *Hippotherium* was very early derived and identified in Central and Western Europe at the base of the Vallesian (MN9), by 11.0 Ma. An early appearing hipparion in China was *"Hipparion" weihoense* which we refer in this contribution to *Hippotherium weihoense* because of its close metric and character state identity to Central European early Vallesian *Hippotherium*. This systematic referral extends the biogeographic range of *Hippotherium* now from China, through Central Europe and Spain (Qiu et al. 1987; Woodburne 2007; Zhegallo 1978; Bernor et al. 1988, 1996, 2017; Woodburne et al. 1996). By the late Vallesian, Old World hipparionines underwent an extensive evolutionary radiation across Eurasia and Africa including several distinct lineages: *Hippotherium, Cremohipparion, Hipparion* s.s., *Sivalhippus, Eurygnathohippus, Baryhipparion, Plesiohipparion* and *Proboscidipparion* (Qiu et al. 1987; Bernor et al. 1996; 2010; Bernor and Sun 2015). We recognize herein a new monospecific Chinese lineage *Shanxihippus dermatorhinus* formally referred to the genus *Hipparion* (sensu lato; Sefve 1927; Qiu et al. 1987; Bernor et al. 1990).

Sefve (1927) first reported two species with highly specialized constructed nasal-snout regions: *Hipparion dermatorhium* and *Proboscidipparion sinense*. In his monograph, he described the specimens of these two species, but did not discuss their rela-

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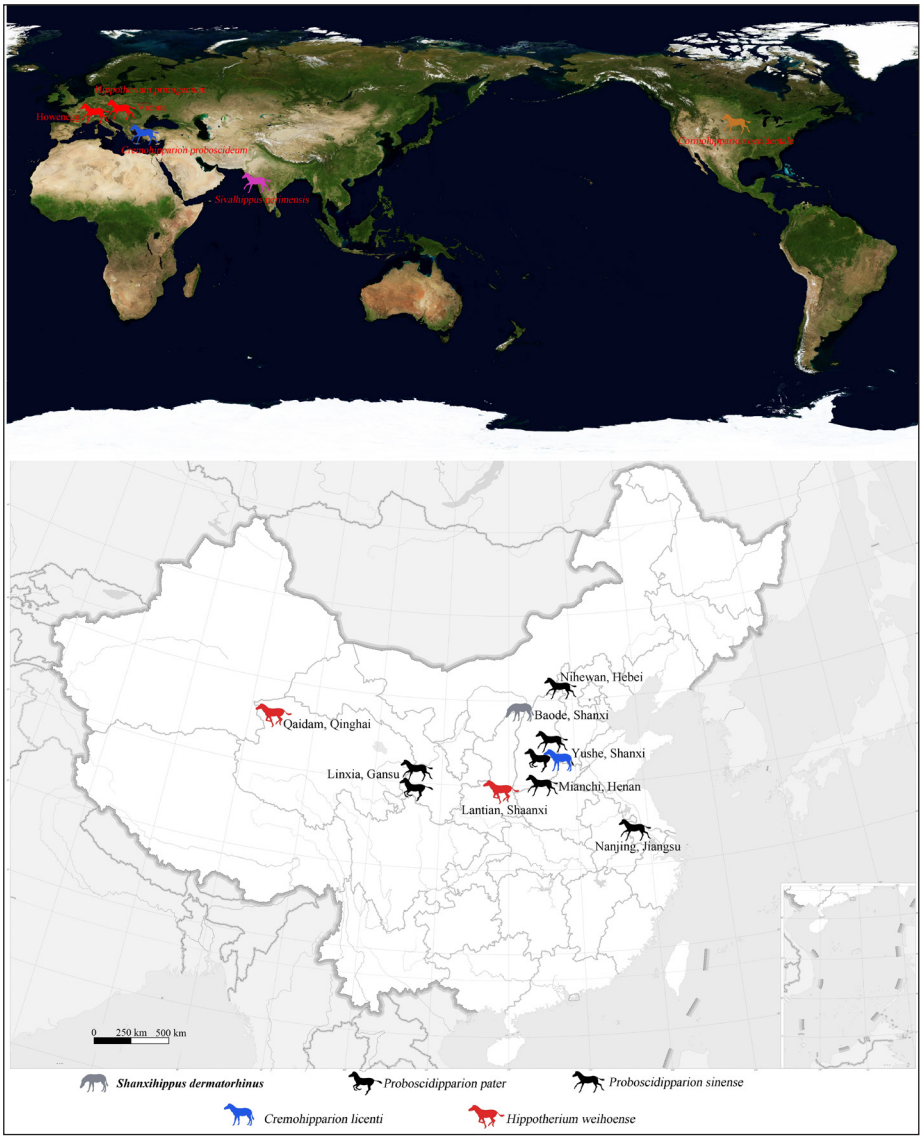

Fig. 1 - Geographic Locator Map (include all localities of specimens analyzed in Log10 analysis. Species are color coded and have different standing and/or running positions: *Shanxihippus dermatorhinus* (Gray, China, lower map only, standing, neck bent feeding); *Proboscidipparion pater* (Black, China, forelimbs folded caudally lower map only), *Proboscidipparion sinense* (Black, China, forelimbs stretched outward, lower map only), *Cremohipparion licenti* (Blue, China, lower map only, standing), *Cremohipparion proboscideum* (Blue, Greece, upper map only, standing), *Hippotherium weihoense* (Red, China only, running), *Hippotherium primigenium* (Red, Austria and Germany, upper map only, walking), *Sivalhippus perimensis* (Purple, Pakistan, upper map only, walking), *Cormohipparion occidentale* (Orange, North America, upper map only, walking).

tionship. Teilhard de Chardin and Piveteau (1930) described a broken juvenile skull of *Proboscidipparion sinense* and recognized this as a subgenus, *Hipparion Proboscidipparion sinense*. Qiu et al. (1987) undertook a systematic revision of Chinese hipparions recognizing several subgenera of the genus *Hipparion* following in part Sefve (1927) and Teilhard de Chardin and Piveteau (1930). Specifically, Qiu et al. (1987) regarded Sefve's highly derived species *Proboscidipparion sinense* as a subgenus of *Hipparion*. Qiu et al. (1987) also recognized a second, more primitive species of *Proboscidipparion* as *Hipparion* (= *Proboscidipparion) pater*.

Qiu et al. (1987) also reported two new specimens of a taxon with highly retracted nasals *Hipparion dermatorhium* Sefve 1927 and first hypothesized the relation between it and *Proboscidipparion*. Deng (2012) reported a newly discovered complete juvenile skull of *Proboscidipparion sinense* from the Linxia Basin and argued that *P. sinense* and *H. dermatorhinum* shared several characters such as the widely exposed lacrimal bone on the facial surface, deep buccinator fossa, sharp nasal process of the premaxillary bone between the nasal and maxillary bones, and well developed lateral part of the nasal bone surrounding the nasal notch and supported the phylogenetic relationship between them. Qiu et al. (1987) also erected a new subgenus *Hipparion* (*Cremohipparion*) and its type species *Hipparion* (*Cremohipparion) licenti*. Bernor and Tobien (1989) raised *Cremohipparion* to generic rank reporting a new small species from Samos, *C. nikosi*. Subsequently, Bernor et al. (1996) recognized several species of *Cremohipparion* ranging from the Eastern Mediterranean to China and the Siwaliks (Wolf et al., 2013), including Chinese Yushe Basin *Cremohipparion licenti*. *Cremohipparion li-*

centi shares contraction of the nasal bones with *S. dermatorhinus* and *P. sinense* but with differing surrounding morphology of the face and rostrum. In this study, we compare and analyze primitive New and Old World taxa relevant to the radiation of the *Shanxihippus, Cremohipparion* and *Proboscidipparion* clades using a combination of metric and character state data. We further develop the likely feeding adaptations and biogeography of these derived forms.

Figure 1 is a locator map for the occurrence of *Shanxihippus dermatorhinus* and our comparative analytical sample, including *Cormohipparion occidentale* (North America), *Hippotherium primigenium* (Vienna Basin Pannonian D-E and Hoewenegg, Germany), *Hippotherium weihoense* (China), *Sivalhippus perimensis* (Pakistan), *Cremohipparion proboscideum* (Greece), *Cremohipparion licenti* (China), *Proboscidipparion pater* and *Proboscidipparion sinense* (China).

Systematic 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, 2010, 2016).

Hipparionini (or, the common name hipparionines) - a tribe of Equidae with an isolated protocone on maxillary premolar and molar teeth and tridactyl feet. Herein, we recognize the following North American, Eurasian and African lineages that they have held to generic rank, including: *Cormohipparion*, *Neohipparion*, *Nannippus*, *Pseudhipparion*, *Hippotherium*, *Cremohipparion*, *Hipparion*, *Sivalhippus*, *Eurygnathohippus* (= a senior synonym of *Stylohipparion*), *Proboscidipparion* and *Plesiohipparion*. These hipparionine lineages have recently been reviewed by Qiu et al. (1987), Bernor & White (2009), Bernor et al. (2010, 2013, 2014, 2015), Armour-Chelu & Bernor (2011), Wolf et al. (2013) and Bernor & Sun (2015). Qiu et al. (1987) and Deng (2012) have held these taxonomic rankings to the subgenus rank, such as *Hipparion* (*Proboscidipparion*) *pater*. We follow Bernor and co-authors recognizing these as multispecies lineages warranting genus-level ranking.

Metric Procedures

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

Those specimens that we refer to *Shanxihippus dermatorhinus* and other hipparions with highly specialized constructed nasal-snout regions are listed in Tab. 1 with accompanying information on their geographic location and chronologic age. Tab. 2 includes measurements on the variables used in the Log10 ratio diagrams.

Tabs. 3-6 list standard measurements for specimens (after Bernor et al. 1997) referred to these Chinese species: Tab. 3, skulls; Tab. 4, mandibles; Tab. 5, maxillary dentitions; Tab. 6, mandibular dentitions. (All tabs are grouped in Appendix 1).

Character State Distribution

Tab. 7 (Appendix 1 and 2) summarizes the characters state distribution of *Shanxihippus dermatorhinus* and our comparative sample analysed herein. This is updated from a series of publications by Bernor et al. (1988, 1989, 1990, 1996, 1997, 2003, 2013, 2017) and Sun et al. (2018). The new additional characters of the maxillary and mandibular cheek teeth follow their definition in Bernor et al. (2017), and are recorded as unordered states (a, b, c, . . . etc.). When a character state is followed by a slash (/), we record a state that is either intermediate (i.e., a/ is intermediate between states a and b), or variably expressed (a, b) in the species hypodigm. These tables have ordered specimens into morphological groups based on their shared states. Morphological groups have been cross checked by size comparisons and the stage of cheek tooth wear was evaluated so that a given specimen was not excluded from a group because of ontogenetic variation.

Abbreviations

We use the following abbreviations in this manuscript:

Ma: mega-annum in the geochronologic time scale. Ages in m.y. are based on radioisotopic analyses or magnetostratigraphic analyses.

Measurement Table Abbreviations Sex: M = male; F = female; 3 = unknown.

Sex can be defined by the size of a canine tooth, male being large, female being small.

Side: lt. = left; rt. = right.

Cranial abbreviations: IOF = infraorbital foramen; POB = preorbital bar; POF = preorbital fossa.

Element abbreviations in tables: tx = maxillary tooth; tm = mandibular tooth; skull = skull; mand = mandible; MCIII = metacarpal III; MTIII – metatarsal III.

M1-M38 refers to measurements as described by Eisenmann et al. (1988) and Bernor et al. (1997).

C1-C53 refers to Characters 1-53.

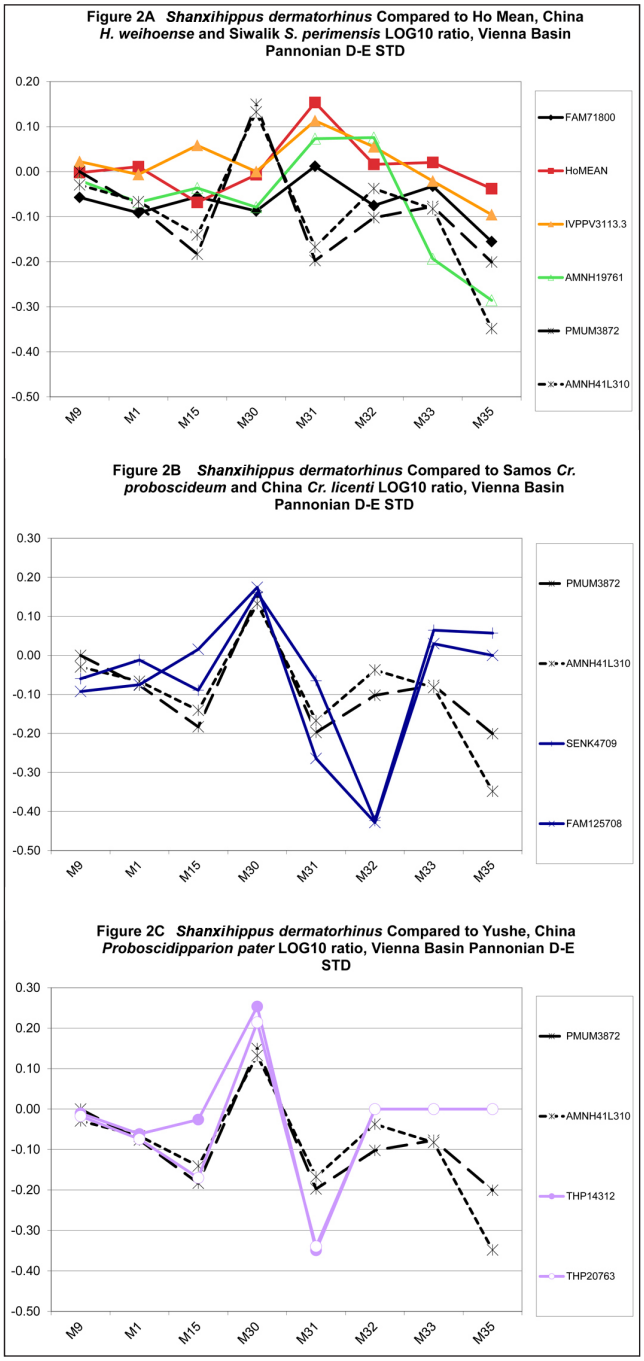

Fig. 2 - Log 10 analyses. A) Comparison of *S. dermatorhinus, C. occidentale, H. primigenium, H. weihoense, S. perimensis.* B) Comparison of *S. dermatorhinus, C. proboscideum* and *C. licenti.* C) Comparison of *S. dermatorhinus* to *P. pater* and *P. sinense.*

Institutional Abbreviations

AMNH – American Museum of Natural History, New York

IVPP - Institute of Vertebrate Paleontology and Paleoanthropology; V = vertebrate specimen

PMU – Museum of Evolution, Uppsala University (formerly the Paleontological Museum of Uppsala), M = vertebrate specimen.

THP – Tientsin Hoangho Paiho, from old name of Tianjin Natural History Museum, Tianjin.

HMV- the vertebrate collection of the Hezheng Paleozoological Museum, Hezheng, Gansu.

Terminology and measurements: All follow Sisson (1953), Eisenmann et al. (1988) and Bernor et al. (1997).

Statistical Analysis - Log 10 Ratio Analyses

We analyze the following taxa in this investigation (Fig. 2 A-C): the primitive taxa, *Cormohipparion occidentale* from North America (FAM71800,10.8 Ma., Bernor et al. 2003), *Hippotherium primigenium* from Hoewenegg Germany (10.3 Ma, Bernor et al. 1997; mean measurements for this quarry sample used), *Hippotherium weihoense* from Lantian, China (IVPPV3113.3, 10.5 Ma; Qiu et al. 1987) and *Sivalhippus perimensis* from the Potwar Plateau, Pakistan (AMNH19761, 8 Ma; Bernor and Hussain 1985 and Wolf et al. 2013). We also analyze two species of the *Cremohipparion* lineage, *C. proboscideum* from Samos, Greece (SENK4709, ca. 8.2-6.7 Ma most of sample from Q1, 7.1 Ma; Vlachou & Koufos 2009) and *C. licenti* from Yushe Basin, China (FAM125708, ca. 4.0 Ma; Qiu et al. 1987) and *Proboscideum licenti* from the Yushe Basin, China (THP14312, THP20763; 5.0 Ma; Qiu et al., 1987). We do not anaylze *P. sinense* (2 Ma) from Henan, China (Sefve 1927; Bernor et al. 1990) and Linxia Basin, China (Deng et al. 2013) due to the lack of a prominent nasal bone. *Shanxihippus dermatorhinus* (PMUM3872 and AMNH41L310) are analysed in all three log10 plots (Figs 2A-C). . Pannonian D-E *Hippotherium primigenium* NHMWA4229 (Ca. 10.5 Ma) is used as the Log10 standard.

Fig. 2A compares China *S. dermatorhinus* to North American *Cormohipparion occidentale*, Hoewenegg *Hippotherium primigenium,* China *Hippotherium weihoense,* Pakistan *Sivalhippus perimensis.* The log10 standard is calculated using Vienna Basin Pannonian E *Hippotherium primigenium* NHMW4229 for Figs 2A-2C. Cheek tooth length (M9) is somewhat less in *S. dermatorhinus* than *Hippotherium* and *Sivalhippus* and slightly greater than *C. occidentale.* Muzzle length (M1) is similar in *H. primigenium* and *H. weihoense* and similarly reduced in *C. occidentale, S. perimensis* and *S. dermatorhinus. Hippotherium weihoense* has the greatest muzzle breadth (M15), whereas *C, occidentale,* Hoewenegg *H. primigenium* and *S. perimensis* have muzzle widths less than the Log 10 standard. *Shanxihippus dermatorhinus* has the narrowest muzzle width. Whereas the Log 10 length of naso-incisival notch (M30) is the same for *H. primigenium* and *H. weihoense,* it is less in *C. occidentale* and *S. perimensis* than *Hippotherium* from Central Europe and China. *Shanxihippus dermatorhinus* is strongly divergent from *C. occidentale*, *H. primigenium*, *H. weiho-*

ense and *S. perimensis* in its greatly increased length of the naso-incisival notch (M30): the nasal bones are strongly retracted. Likewise, *S. dermatorhinus* has a correspondingly strong decrease in cheek length (M31) from the posterior limit of the narial opening to the most anterior point of the orbit compared to *Cormohipparion, Hippotherium* and *Sivalhippus.* POB length (M32) is longest in *S. perimensis,* similar between the two *Hippotherium* species and lowest in *C. occidentale* and *S. dermatorhinus.* Maximum length of the POF (M33) is greatest in *H. primigenium* with Hoewenegg and the log10 standard being very similar; slightly less in *H. weihoense* and *C. occidentale,* being slightly reduced further in *S. dermatorhinus* and strongly reduced in *S. perimensis.* Height of the POF (M35) is greatest in *Hippotherium* log 10 standard and Hoewenegg, somewhat less in *H. weihoense,* further reduced in *C. occidentali*, and least in *S. dermatorhinus* and *S. perimensis* which together have the lowest height measurements. Height of the preorbital fossa directly reflects cheek tooth crown height: the greater the dorso-ventral height (and position relative to the facial-maxillary crest), the lower the crown height since the cheek tooth roots are limited by the ventral extent of the POF.

Fig. 2B compares *Shanxihippus dermatorhinus* with Greek *Cremohipparion proboscideum* and China *Cremohipparion licenti.* Most variables are similar except for length of POB (M32) which is much greater in *Shanxihippus* than either species of *Cremohipparion* and POF length (M33) and height (M35) which is much greater in the two *Cremohipparion* species. *Cremohipparion proboscideum* has a muzzle breadth dimension (M15) which is very close to *S. dermatorhinus* except *S. dermatorhinus* AMNH125708 which is somewhat elevated (perhaps due to some crushing). The greater dorsoventral depth and length of *Cremohipparion proboscideum* and *C. licenti* POF reflects its lower crown height than *S. dermatorhinus.*

Fig. 2C compares *S. dermatorhinus* to two specimens of *Proboscidipparion pater* which lacks both lack a POB and POF, disallowing measurements 32-35. *Proboscidipparion sinense* has no nasal notch with the nasal bones retracted superior to the posterior cheek tooth row (Bernor et al. 1990) disallowing M30 and 31; therefore we do not plot measurements for *P. sinense* herein. *Shanxihippus dermatorhinus* compares closely in its measurements with *P. pater* for cheek tooth row length (M9), muzzle length (M1) and THP20763 *P. pater* muzzle width (M15); muzzle width is greater for THP14312 *P. pater.* The length from the posterior limit of the nasal notch to the anterior point of the orbit (M31) is strongly reduced in *P. pater* compared both to *Shanxihippus* and the *Hippotherium primigenium* Log 10 standard reflecting its extreme nasal retraction.

Cladistic Analysis

For our cladistic analysis we created a new data matrix, which includes 14 taxa, and 45 characters of the 53 listed in Tab. 7 revised from Bernor et al. (1988, 1989, 1990, 1996, 1997, 2003, 2012, 2017), Wolf et al. (2013) and Sun et al. (2018) (Appendix 1 and 2). Characters 2, 3, 11, 19, 23, 28, 30, 31 were not included in the analysis because they are invariable within the ingroup taxa. The data matrix was polarized using four North American outgroups, consecutively further removed from the most primitive Old World hipparions: *Cormohipparion occidentale, Cormohipparion quinni, Merychippus insignis* and *Parahippus leonensis.* The phylogenetic analysis was calculated using TNT 1.1 with a traditional research method (Tree Analysis using New Technology; Goloboff et al. 2008), 1000 replications and the trees-bisection-reconnection branch-swapping algorithm (TBR). All characters are equally weighted and non-additive.Gaps were treated as "missing" and multistate taxa interpreted as polymorphism. The data matrix was compiled in Mesquite version 3.04 (Maddison & Maddison 2015). The reported results were based on the most parsimonious trees (MPTs).

Systematics

Order **Perissodactyla** Owen, 1848
Suborder **Hippomorpha** Wood, 1937
Superfamily Equoidea Hay, 1902
Family Equidae Gray, 1821
Subfamily Equinae Steinmann & Doderlein, 1890
Tribe Hipparionini Quinn, 1955
Genus *Shanxihippus* gen. nov.

Type-species: *Shanxihippus dermatorhinus* comb. nov.

Etymology: this taxon is thus far only known from Shanxi Province, China.

Age: Late Miocene, ca. 5.7 Ma.

Geographic Range: Baode, Shanxi, China

Diagnosis (modified from Bernor et al. 1990)**:** * indicates

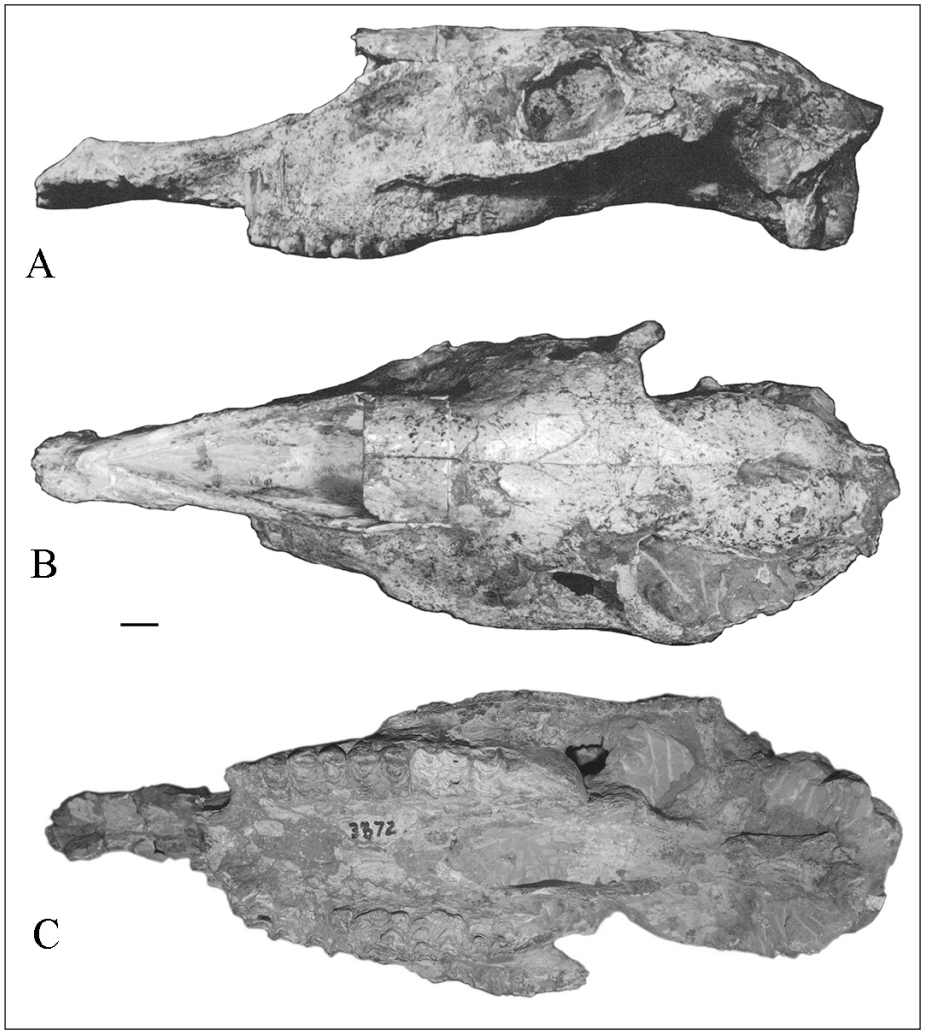

Fig. 3 - Lectotype *Shanxihippus dermatorhinus*. PMU M3872 skull. A) lateral view; B) dorsal view; C) ventral view. Scale bar = 2 cm.

primitive characters for Old World hipparions; ** indicates derived characters for Old World hipparions; *** indicates autapomorphies for *Shanxihippus*.

A medium to large hipparion with prominent POF that is subtriangularly shaped*, anteroposteriorly oriented*, with moderate posterior pocketing, strong peripheral outline* and prominent anterior rim*. Preorbital bar is long with anterior edge of lacrimal placed more than half the distance from the anterior orbital rim to the posterior rim of the fossa.*. Nasal notch is sharply retracted and placed above P4***. Rostral region is elongate, slender and V-shaped from proximal to distal extent***. Maximum cheek tooth crown height is 60 mm+. ** Maxillary cheek teeth are complex, with several deeply amplified plications*; pre- and postfossettes linked in P2* and not in P3-M3**; protocones are lenticular shaped***, not lingually flattened** and lacking protoconal spur**. Mandibular incisors are not grooved*; cheek tooth metaconids are rounded* while metastylids are rounded to angular on the mesial surface**; metastylid spur occurs on p3 and p4* but not p2 or the molars**. Pli caballinids are rudimentary on p3 and p4* while being absent on the other cheek teeth**. Ectostylids are absent on adult cheek teeth**. Premolar linguaflexids are shallow* while molar linguaflexids are shallow U-shaped**. Postcranial anatomy is unknown.

Differential Diagnosis: * indicates primitive characters for Old World hipparions; ** indicates derived characters for Old World hipparions; *** indicates autapomorphies for the clades discussed herein.

Shanxihippus is unique amongst Old World hipparionines in its anterior facial anatomy having sharply retracted nasals (to P4) coinciding with an elongate snout that is V-shaped narrowing sharply at the incisor region*** and with unflattened, lenticular shaped protocones***. *Proboscidipparion pater and P. licenti* differ from *Shanxihippus* in their lack of a POF**, infraorbital foramen placed high on the maxilla near the orbit**, a premaxilla that is not V-shaped, but straight and dorsally convex in the incisor region** with protocones that are lingually flattened labial rounded (*P. pater*)*, or triangular-elongate (*P. sinense*)** and cheek tooth linguaflexids that have a broader U-shape**. *Cremohipparion* species (specifically *C. mediterraneum, C. proboscideum, C. licenti*) differ from *Shanxihippus dermatorhinus* in having a dorsoventrally deeper POF ** , presence of a caninus (= intermediate) fossa**, and in the case of *C. licenti* nasal bones retracted to M1**, a POF with internal pits** and a malar fossa** (only Old World taxon with these last two characters). *Cremohipparion* has a lower cheek tooth crown height*, correlated with the dorsoventrally expanded POF**, and simpler maxillary cheek tooth plications**. *Sivalhippus* species differ from *Shanxihippus dermatorhinus* in having a POF placed farther anterior on the face**, being much shorter antero-posteriorly and dorsoventrally**, having the anterior limit of the lacrimal placed more posteriorly** and lacking nasal retraction beyond the mesial limit of P2*. Likewise, *Hippotherium primigenium* and *H. weihoense* as well as Eurasian and African taxa *Hipparion* s.s., *Baryhipparion, Plesiohipparion* and *Eurygnathohippus* all lack retracted nasals beyond mesial border of P2*. The *Hipparion, Plesiohipparion* and *Eurygnathohippus* lineages lose their POF's entirely in advanced species. **

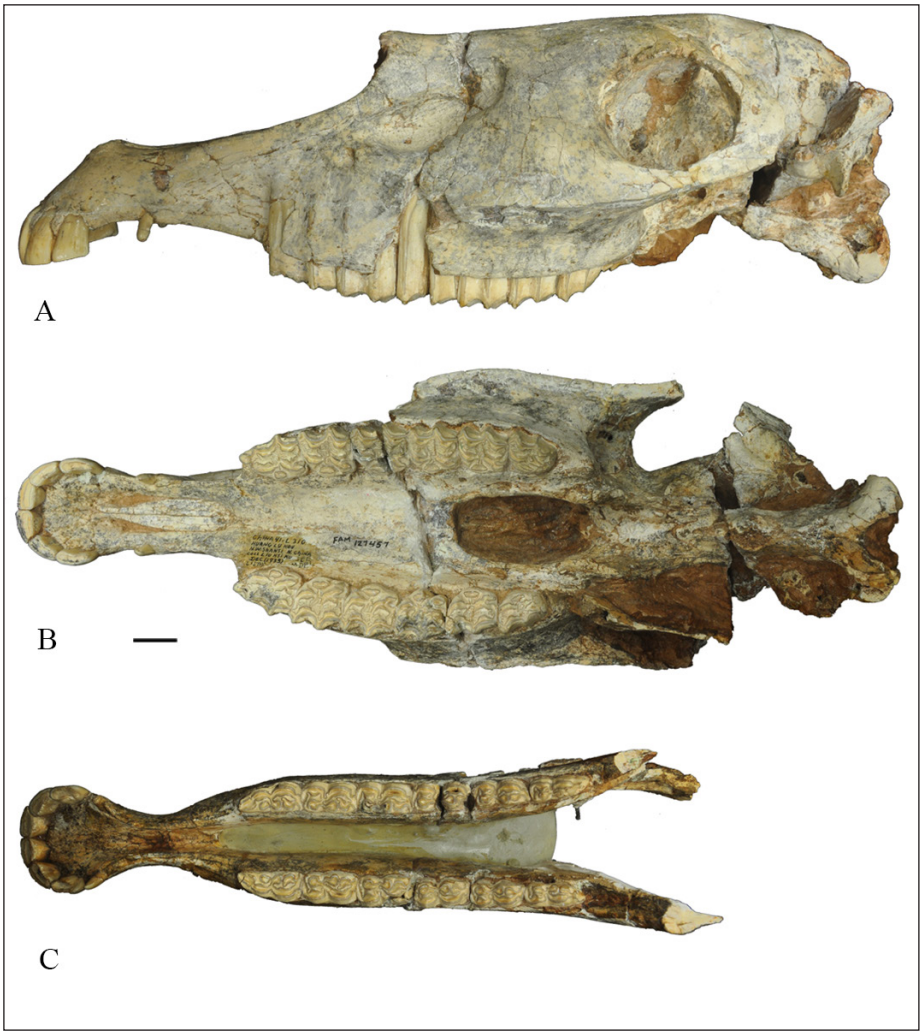

Fig. 4 - AMNH 41 L310 *Shanxihippus dermatorhinus*. A) lateral view skull; B) occlusal view maxillary dentition; C) occlusal view mandibular dentition. Scale bar = 2 cm.

Shanxihippus dermatorhinus comb. nov.

Hipparion dermatorhinum Sefve, 1927: p. 13; Figs. 1-3; Pl.1.
Hipparion dermatorhinum Qiu et al., 1987 (in part) : p.130; Fig. 56; Pls. XLI-XLIII, XLVI.
"Hipparion" dermatorhinum Bernor et al., 1990: p. 33; Figs. 13, 14.

Lectotype (Bernor et al. 1990): PMU M 3872, a nearly complete juvenile skull with dentition, housed in the Paleontological, Museum, University of Uppsala, Sweden. (Sefve, 1927: Taf. I, Fig. 1-3).

Lectotype locality: Locality 30, Baode County, Shanxi Province, China (Zdansky, 1923). Age of Locality 30 has recently been calibrated using magnetostratigraphy with chron C3r, with an age estimate of 5.7 Ma (Kaakinen et al., 2013). This is younger than a previous magnetostratigraphic correlation by Yue et al. (2004) of 7.0 – 6.5 Ma. We take the age to be between 7.0 and 5.7 Ma.

Diagnosis: as for the genus.

Description. PMU M3872, the Lectotype skull of *Shanxihippus dermatorhinus,* is a juvenile with a complete premaxilla, lacking incisors and canine but with DP2-4, M1 and M2 emerging from its crypt (Fig. 3 A-C). The muzzle length (M1) is 114.5 mm, elongate, narrow, with a narrow incisor arcade (M15 = 36.0 mm) and as viewed dorsally describes a sharp V-shape from the wide proximal narial opening to its most anterior limit (re: Fig. 3B). POB length is 37.3 mm. POF has a length 64.3 mm and has a dorsal-ventral height 35.4 mm. The remainder of the skull morphology conforms to the species diagnosis given above. Maximum cheek tooth crown height is 60 mm+ (18C/D).

AMNH 41 L310 (= AMNH 127457; Bernor et al., 1990, Fig. 14C-D) is an adult female skull with incisors, small canine and P2-M3 (Fig. 4A & B). There is an associated mandibular dentition with p2-m3 (Fig. 4C; Bernor et al., 1990; Fig.14C-E). Skull morphology is as in the PMU Lectotype. Cheek tooth length (M9) is 149.5 mm. The muzzle length (M1) is 117.2 mm., elongate, narrow, with a narrow incisor arcade (M15 = 39.5 mm) and as viewed dorsally describes a sharp V-shape from the wide proximal narial opening to its most anterior limit (re: Fig. 4B). POB length (M32) is 43.3 mm. POF length (M33) is 63.5 mm and has a dorsal-ven-

tral height 25.2 mm. Maximum cheek tooth crown height is 60+ mm (C20CD). Pre- and postfossettes are linked in P2 (C22A) and not in P3-M3 (C22B, overall, C22AB). Pli caballin is single in all cheek teeth (C24B). The remainder of the skull morphology conforms to the species diagnosis given above.

The mandibular dentition of AMNH 41 L310 (Fig. 4C) conforms to the diagnosis given above. Salient features of the mandibular dentition are the mostly rounded metaconids (C33A, C34A) of the premolar and molar dentition, rounded premolar metastylids (C35A) and rounded to angular molar metastylids (C37AC), the prominent metastylid spurs on p3 and p4 (C38A), and the tiny pli caballinids on p3 and p4 (C41B). The metastylid spur and pli caballinids are primitive features found in Vienna Basin Pannonian C *Hippotherium.*

PMU M260 is a juvenile palate with dP1-4, M1 and M2. Its POB length is slightly shorter than the Lectotype, 32.4 mm. POF is shorter than in the Lectotype = 58.2 mm. and has a dorsal-ventral height larger than the Lectotype, 57.8 mm. The distance from the ventral border of the POF to facial maxillary crest is larger, 29.7 mm.

PMU M 259 is a young adult right and left palate fragment with P2-M3, M3 just beginning to wear. It differs from the Lectotype in that its maxillary cheek tooth fossette ornamentation is more complex, with several deeply amplified plications (C21A). Pli caballin is single or occasionally poorly defined double (C24B). Hypocone is frequently encircled by hypoglyph (C25A). Protocone is lingually flattened-labially rounded (C26E).

PMU M 261 is a palate fragment with right and left P2-M1. It differs from the Lectotype in that maxillary cheek tooth fossette ornamentation is complex, with several deeply amplified plications (C21A). Hypocone is frequently encircled by hypoglyph (C25A). Protocone is lingually flattened-labially rounded (C26E).

Remarks. Bernor et al. (1988) have included *"Hipparion"* (= *Shanxihippus*) *dermatorhinus* in their phylogeny of Group 1 horses (sensu Woodbume and Bernor 1980; Bemor 1985, and Bemor and Hussain 1985) and found that the group is paraphyletic with *S. dermatorhinus* possibly being a distinct, monospecific lineage, geographically restricted to China. Bernor et al. (1990) indicated this species retains primitive features of the POB and POF including its subtriangular shape and anteroventral orientation. *Shanxihippus dermatorhinus* also has distinct autapomorphies of the facial region, including its very strongly retracted nasal notch and markedly lengthened, anteriorly narrowed V- shaped premaxilla. Review of AMNH 41L 310 (= AMNH127457) reveals primitive features of P2 pre- and postfossette linkage, occurrence of metastylid spurs and small pli caballinids on p3 and p4 as is found in the most primitive *Hippotherium* from Vienna Basin Pannonian C (Bernor et al. 2017).

Our Log 10 ratio analysis includes cranial dimensions of primitive North American *Cormohipparion occidentale* (Bernor et al. 2003; Woodburne 2007), Vienna Basin Pannonian D-E *Hippotherium primigenium* (NHMWA4229 Log 10 standard; Bernor et al. 1988), China *Hippotherium weihoense* (Qiu et al. 1987 recognized herein as a member of *Hippotherium*), Pakistan *Sivalhippus perimensis* (Bernor and Hussain 1985; Wolf et al. 2013); Samos, Greece *Cremohipparion proboscideum;* Yushe Basin, China *Cremohipparion licenti;* Yushe Basin, China *Proboscidipparion pater* and Henan and Linxia Basin, China *Proboscidipparion sinense.*

Tab. 7 provides our summary of the character state distribution of the taxa and specimens considered in this study. It follows refinements made in a sequence of articles, of which this is the latest (Bernor et al. 1988, 1990, 1996, 1997, 2003, 2017; Sun et al. 2018). We recognize a total of 53 character states, labelled herein C1-53 that are distributed among 4 North American outgroup taxa *Parahippus leonensis, Merychippus insignis, Cormohipparion quinni* and *Cormohipparion occidentale* and species of five Eurasian genera: *Hippotherium, Sivalhippus, Shanxihippus, Cremohipparion* and *Proboscidipparion.*

Cormohipparion occidentale, *Hippotherium primigenium* and *Hippotherium weihoense* are closely related lineages (Figs 5A-E) recently reviewed by Woodburne (2007, 2009) and Bernor et al. (2017). These lineages are virtually identical across facial characters (C1-C16) except *H. weihoense* which an antero-posteriorly oriented POF (C4E) and nasal notch near anterior margin of P2 (15C). *Sivalhippus perimensis* is likely derived from the *Cormohipparion-Hippotherium* clade differing in having a very elongate preorbital bar (C1F) and a reduced, egg-shaped and anteroposteriorly oriented POF (C4F). In maxillary tooth morphology (C17-C32), *C. occidentale, H. primigenium* and *H. weihoense* are likewise very similar, except: *H. primi-*

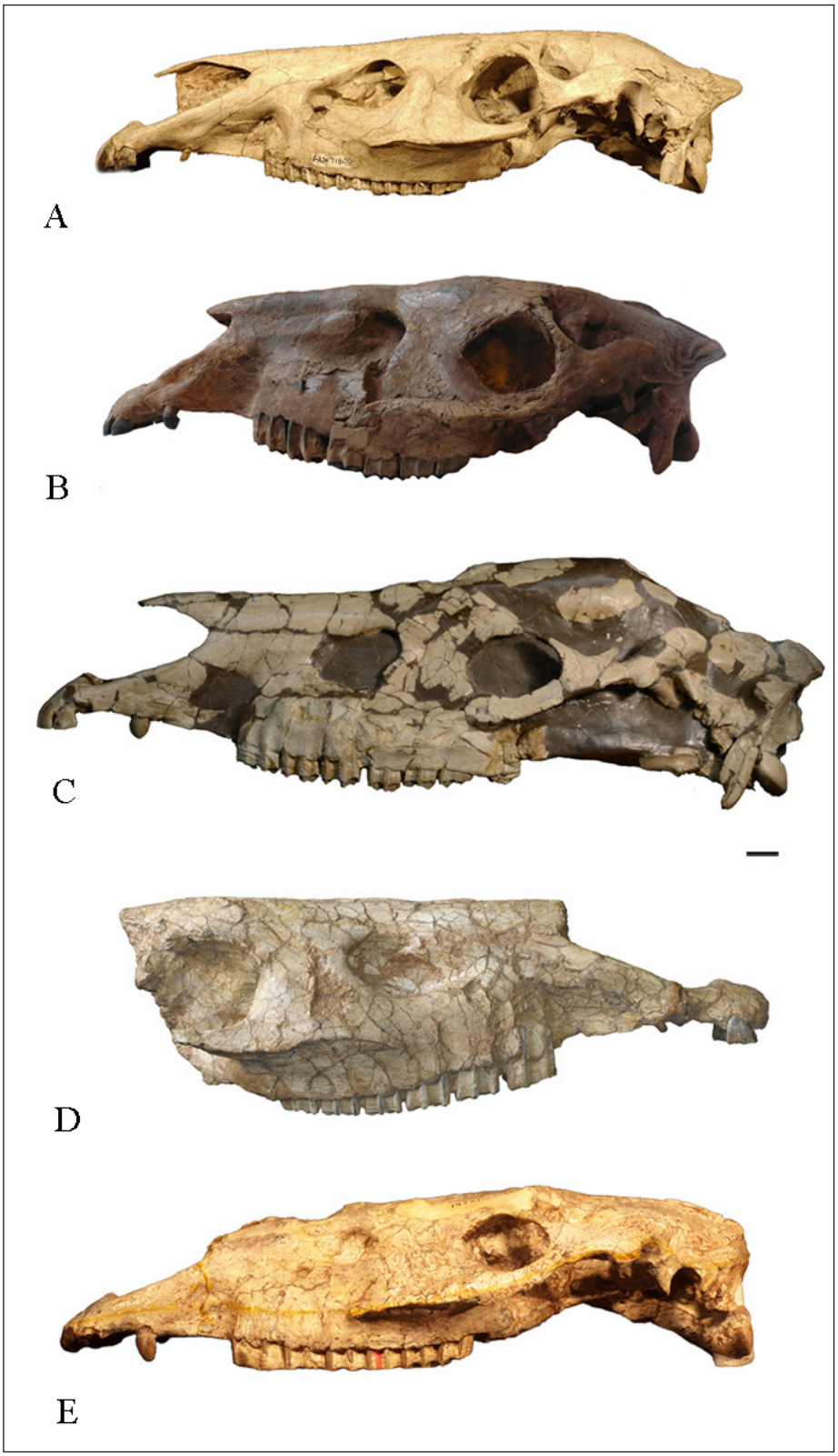

Fig. 5 - A) *Cormohipparion occidentale* FAM71800, skull lateral view; B) *Hippotherium primigenium* NHMW4229 skull lateral view; C) *Hippotherium primigenium* Ho A skull lateral view; D) *Hippotherium weihoense* IVPPV3113.3 skull lateral view; E) *Sivalhippus perimensis* AMNH19761 skull lateral view.
Scale bar = 2 cm.

genium often retains a dP1/dp1 into adult stage of development (C17AB). *Hippotherium primigenium, H. weihoense* and *S. perimensis* have more complex plications of cheek tooth pre- and postfossettes (C19A) than *C. occidentale* (C19B). Also, *C. occidentale* and *H. primigenium* frequently express the primitive condition of pre- and postfossette confluence of the opposing borders (C22AB). Pli caballin morphology varies from complex, to double to single (C24CAB) amongst *Cormohipparion occidentale* and *Hippotherium primigenium,* being more consistently double in *H. weihoense* and *S. perimensis.* Protocone shape is mo-

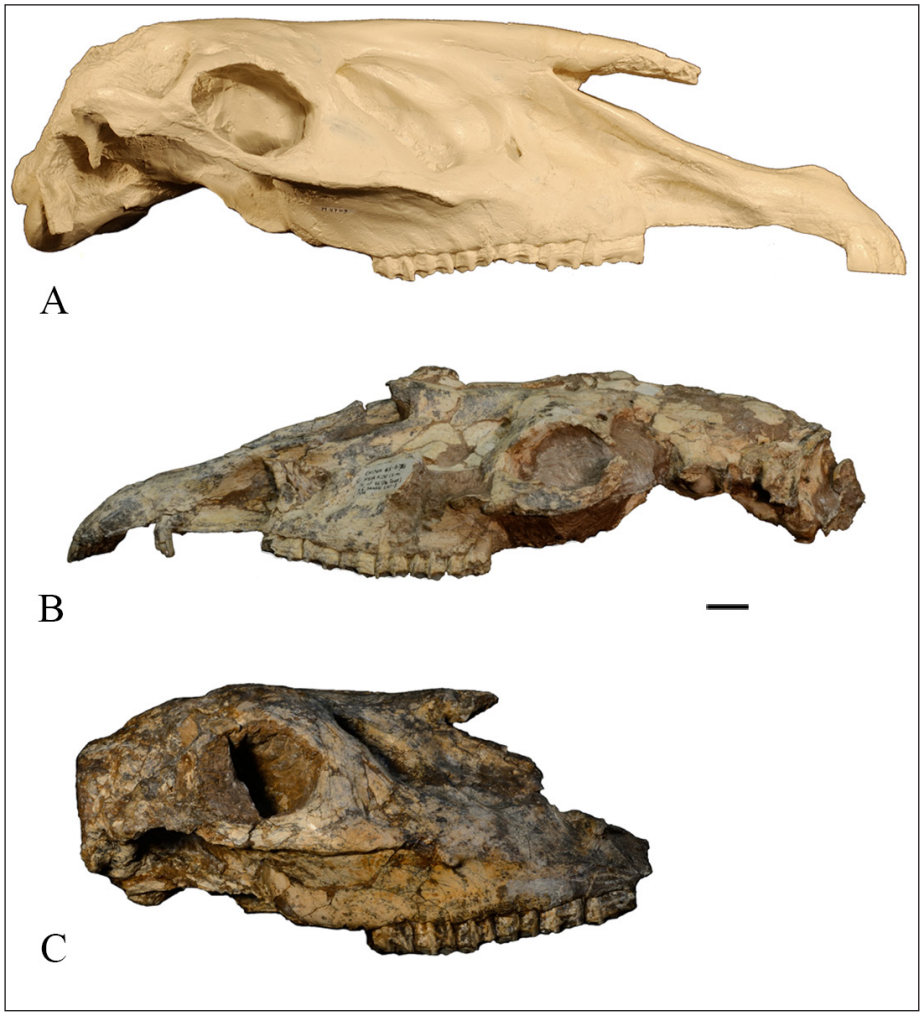

Fig. 6 - A) *Cremohipparion proboscideum* SENK4709 specimen skull lateral view; B) *Cremohipparion licenti* AMNH125708 specimen, skull lateral view; C) *Cremohipparion licenti* THP20764 type specimen, skull lateral view.
Scale bar = 2 cm.

stly lingually flattened and labially rounded (C26E) in a middle stage of wear in *Hippotherium* and *Sivalhippus* while being more elongate oval (C26D) in *C. occidentale* which Bernor et al. (2003) propose as the primitive condition for Old World hipparion. Lingual flattening of the protocone (C27) and isolation of the protocone from the protoloph (C24A) are persistent features of *Cormohipparion, Hippotherium, Sivalhippus* and the other hipparion taxa under consideration in this contribution. The variable presence of a protoconal spur in *C. occidentale* and *H. primigenium* (C29B/C) and not *H. weihoense* and *S. perimense* (C29C) is a primitive character for Old World hipparions. Likewise, all Old World hipparions generally have premolar (C30B) and molar (C31B) protocones that are more lingually placed than the hypocones on P2-M3. P2/p2 anterostyle/anterostylid is elongate (C32U/C32L= A) on these taxa. When known, mandibular incisors are not grooved (C33A), they are curved (C34A) and I3 is elongate but not labiolingually constricted (C35A). When known, premolar (C36A) and molar (C37A) metaconids are rounded; premolar metastylids are rounded to square shape (C38A/E); premolar metastylid spur varies in its presence in *H. primigenium* but is absent in *S. perimensis* (C43AB)*;* molar metastylid is square shaped (C40E) in *H. primigenium* and *S. perimensis*; metastylid spur is variably present or absent (C41A/B) in *H. primigenium* and absent in *S. perimensis* (C41B); premolar ectoflexid primitively variably separates metaconid and metastylid in the premolars (C42AB) in *H. primigenium* and *S. perimensis* and consistently separates metaconid and metastylid in the molars (C43B) in *H. primigenium* and *S. perimensis*. Pli caballinid is rudimentary to absent (C44BC) in *H. primigenium* and *S. perimensis*. Protostylid is absent on the occlusal surface of *C. occidentale* (C45B), present on the occlusal surface and present as an enclosed enamel ring on *H. primigenium* (C45A) and has a strong columnar morphology (C45C) in *S. perimensis*. Protostylid orientation is vertical in all of these taxa (C46C & D). Whereas Vienna Basin Pannonian C hipparions frequently have small ectostylids at the base of their cheek teeth (C47A; Bernor et al. 2017),

Fig. 7 - Skull lateral view of *Proboscidipparion pater* from Yushe Basin, China: A) THP 14312; B) THP 20736. Scale bar = 2 cm.

they are absent in *C. occidentale* (C47B), variable in *H. primigenium* (C47AB) and *S. perimensis* (C47AB which is rarer even than *H. primigenium*). Premolar linguaflexids are shallow in these primitive taxa (C48A). Molar linguaflexids are shallow to shallow U-shape (C49AC) in *C. occidentale* and V to shallow U-shape in *H. primigenium* (C49BC). *Hippotherium primigenium* and *Sivalhippus perimensis* have complex preflexid (C50B) and postflexid (C51B) margins. Postflexid does not invade metaconid/ metastylid junction by the anteriormost portion bending sharply lingually (C52A) and protoconid enamel band is rounded (C53A) in all of these taxa.

Shanxihippus dermatorhinus (Fig. 6) differs from *C. occidentale, H. primigenium* and *S. perimensis* in some critical characters. In *S. dermatorhinus* the reduction of posterior pocketing (C5B) is intermediate between the *Cormohipparion - Hippotherium* clade and *S. perimensis*. In *S. dermatorhinus* the nasal notch is retracted to a level above P4 (C15F) and is unique among all hipparionine lineages in having a premaxilla that is wide proximally and very narrow-V-shape anteriorly (C16B, Fig. 5). Maxillary tooth morphology (C17-32) differs in *S. dermatorhinus* having lenticular shaped protocones (C26J), protocones that are not lingually flattened (C27B) and protoconal spur is highly reduced or absent (C29BC). Mandibular tooth morphology (C33-53) differs in a few minor regards: premolar metaconid is variably rounded/ elongate (C36AB); premolar metastylid varies from being rounded to angular on the mesial surface (C38AC); premolars variably have metastylid spurs (C39AB); molar metastylid is angular on the mesial surface (C40C) and lack metastylid spurs (C41B). Other mandibular cheek tooth characters overlap with the primitive hipparions discussed above.

Cremohipparion proboscideum and *C. licenti* differ from *C. occidentale, H. primigenium, H. weihoense, S. perimensis* and *S. dermatorhinus* in a number of characters (Fig. 6A SENK specimen of *Cprob* + 2 specimens of *C. licenti*). A character uniting all species of *Cremohipparion* is the sharply reduced POB with lacrimal bone invading or touching the posterior border of the POF (C1B). The short preorbital bar corresponds to the expansion of the POF posteriorly accompanied by increased dorso-ventral depth proximally: the POF is extremely deep in this dimension closely approaching the maxillary crest (Figs. 6A-C). *Cremohipparion licenti* is uniquely derived in having POF medial wall with internal pits (C7B), buccinator fossa is pocketed posteriorly (C12B) and there is a distinct malar fossa (C14B). Both *C. proboscideum* and *C. licenti* have distinctly developed caninus fossae (C13B), a character shared with most members of the *Cremohipparion* clade. *Cremohipparion proboscideum* has the nasal notch retracted to above P3 (C15E; re: Fig. 6A), whereas *C. licenti* is further retracted to above M1 (C15G; re: Fig. 6B & C). *Cremohipparion proboscideum* and *C. licenti* express simple complexity of the pre- and post-

fossettes (C21C); there is no linkage of the pre- and postfosettes (C22B); hypoglyphs are moderately to shallowly incised; premolar and molar protocones are oval to elongate-oval shaped (C26CD). Mandibular cheek teeth have not been identified for either *C. proboscideum* or *C. licenti*.

Proboscidipparion is a highly derived hipparion clade that first appears in China in the latest Miocene and extended its range into West Asia by the early Pliocene (Bernor & Sen 2017). There are two Chinese taxa known, the older *P. pater* (ca. 5-4 Ma) and *P. sinense* (ca. 2 Ma). Both *P. pater* and *P. sinense* lack a POF (C1G; C4I, C5E, C6D, C7A, C8E, C9B). In *P. pater* one can clearly distinguish an infraorbital foramen that is placed high on the maxilla near the orbit (C10C). Nasal notch is poorly defined with narial opening posterior to M1 in *P. pater* (C15G) and well posterior to M1 in *P. sinense* (C15H). Premaxilla shape is convex dorsally (C16C) in both *P. pater* and *P. sinense*, a condition unique to hipparionines. The Lectotype *Proboscidipparion sinense* is an adult individual in an advanced stage of wear. Nevertheless, the Lectotype has maxillary cheek teeth that have highly complex pli caballins (C24C) and protocones that are triangular-elongate (C26I). Both specimens of *Proboscidipparion pater* have protocones that are as in *Hippotherium* and *Sivalhippus* being lingually flattened and labially rounded (C26E). The Lectotype *P. sinense,* PMU M3925 mandibular dentition is derived compared to other hipparion clades considered here in the following characters: premolar metaconid is angular on the distal surface (C36C); molar metaconid is angular on the distal surface (C37C); premolar metastylid spur (C39C) and molar metastylid spur (CC41C) are absent; protostylid is absent (C46F); there are no ectostylids (C47B); premolar and molar linguaflexids are deep, broad U-shape (C48D, C49D); preflexids (C50A) and postflexids (C51A) have simple margins; postflexid anterior portion does not bend sharply lingually (C52A) and protoconid enamel band is rounded (C53A).

Phylogenetic Analysis

A cladistic analysis was undertaken to investigate the possible phylogenetic relationships between *Shanxihippus dermatorhinus* and pertinent Eurasian hipparion genera and North American equid outgroups consecutively more primitive: *Cormohipparion occidentale, Cormohipparion quinni, Merychippus insignis* and *Parahippus leonensis*. Four Most Parsimoious Trees (MPTs) were generated (Fig. 8) with the tree length = 81, consistency index = 0.877, and retention index = 0.825. However, only one MPT (Fig. 8A) was accepted. The other three MPTs (Fig. 8B–D) were rejected, because character 15, nasal notch position, is unreasonably reversed. In all of the three rejected MPTs, C15 changes from the state G to E in *Cremohipparion proboscideum* and from G to F in *Shanxihippus* (open circles in Fig. 8B–D). Literal acceptance of this hypothesis implies that in these three cases, the nasal notch first retreated above the level of M1, and then moved forward again. We believe that nasal retraction is convergent in these three distinct genus-level clades. In the remaining tree (Fig. 8A), *Shanxihippus* and *Proboscidipparion* position as sister groups with the supporting character states C40 = C, C50 = A, and C51 = A. This result is contradictory to hypotheses of Qiu et al. (1987) and Deng (2012). Our analysis suggests that the lineage *Shanxihippus* + *Proboscidipparion* might be derived from the India Subcontinent *Sivalhippus* with the synapommorphies C6 = B and C20 = D. This analysis suggests that *Cremohipparion* is the sister group of *Sivalhippus* + *Shanxihippus* + *Proboscidipparion* clades, which indicates that the retraction of the nasal notch in *Cremohipparion* is a convergent character independent to the nasal retraction found in *Shanxihippus* and *Proboscidipparion*. However, all of these groups might be derived from a certain *Hippotherium* species such as *H. weihoense*. *Shanxihippus dermatorhinus* exhibits confluence (linkage) of pre- and postfossettes on P2 (C22A) and variably premolar metastylid spur (C39AB) which are primitive characters shared with *Hippotherium primigenium*.

Discussion

In their study of the late Miocene Sinap hipparion sequence, Bernor et al. (2003) found that the Hans Johnson *Cormohipparion occidentale* (USA, Fig. 5A) was morphologically close both in cranial-dental and postcranial attributes to the oldest and most primitive hipparion in the Sinap local section, *Cormohipparion sinapensis*. Sinap *C. sinapensis* was similar in facial morphology to primitive Central European (Vienna Basin Pannonian E (Fig. 5B), and Hoewenegg, Germany (Fig. 5C), both MN9 ca. 10.3 Ma)

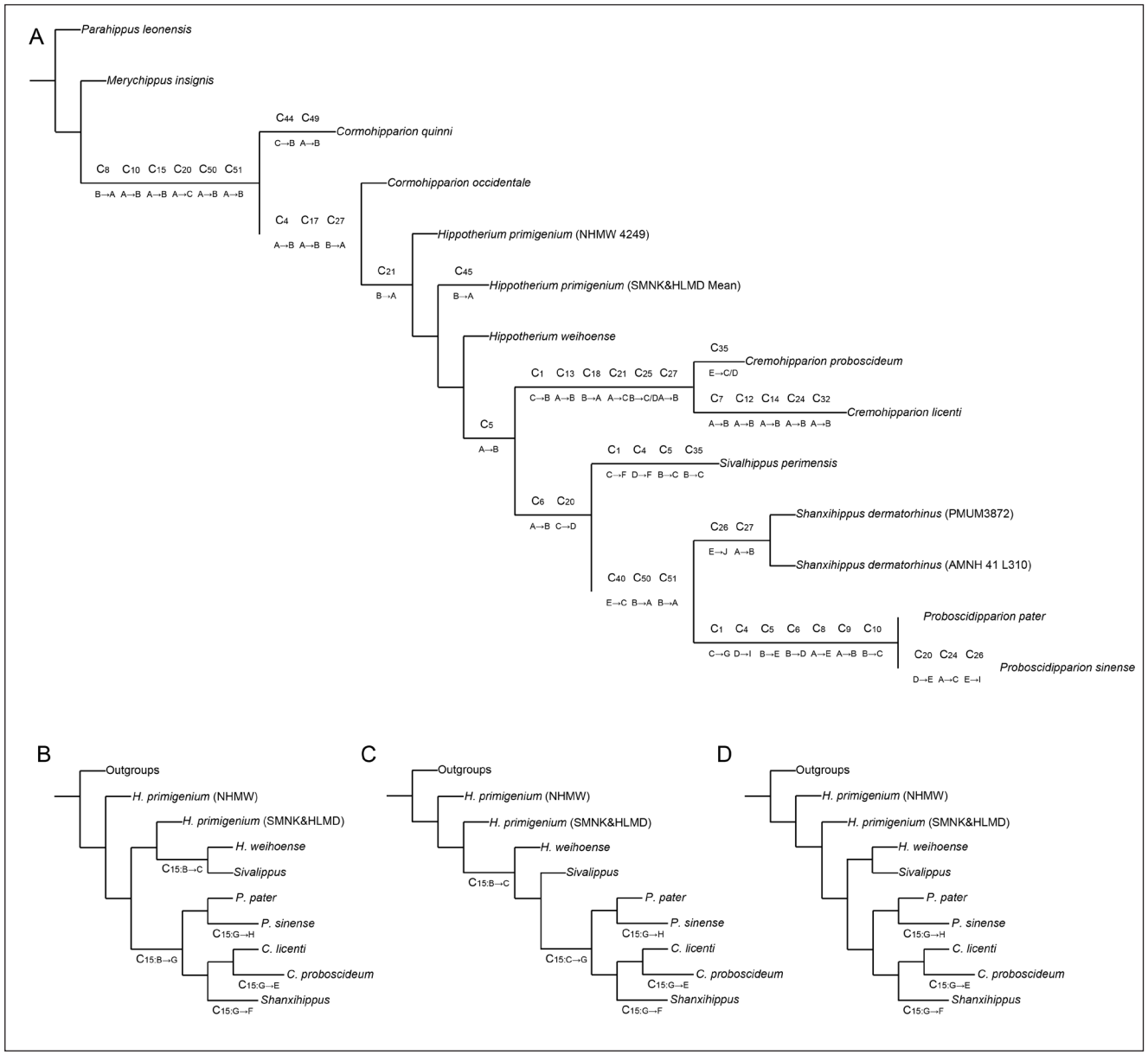

Fig. 8 - The most parsimonious trees (MPTs) showing the phylogenetic reconstruction of the partial Eurasian hipparionine species (tree length = 81, consistency index = 0.877, retention index = 0.825). A, the accepted MPT. The filled circles represent supporting synapomorphies (denoting above the circle) on each node with the changes of character states (denoting below the circle). B–D, the rejected MPTs, because of the reverse of the character 15, the position of the nasal notch. The filled circles represent the retreat of the nasal notch, and the open circles represent the reverse of this character. Character states are shown in Table 7.

Hippotherium primigenium and North African (Bou Hanifia, MN9, Algeria, 10.5 Ma) *"Cormohipparion" africanum* (Bernor & White 2009). While *"C". africanum* was similar in cranial anatomy to *C. occidentale* and *H. primigenium* it is advanced to both in the lengthening of its POF and cheek tooth crown height but very much like *C. sinapensis* in its postcranial proportions.

Woodburne (2009) undertook a study of Vienna Basin Pannonian C hipparions from Atzelsdorf and made early comparisons to a sample of *Cormohipparion* sp. from the California Punchbowl Formation that was shown to be more primitive that *C. occidentale* in several maxillary cheek tooth characters. Bernor et al. (2017) undertook a detailed study of the stratigraphy, geochronology and paleodiet of Vienna Basin Pannonian C hipparions from Gaiselberg, Atzelsdorf and Mariathal and identified a number of primitive characters shared between these hipparions and the California Punchbowl Fm. *Cormohipparion* sp. We find here a number of these primitive lower and upper cheek tooth characters

occur in low frequency in Hoewenegg *Hippotherium primigenium*. A current study is finding that some of these primitive cheek tooth characters occur in primitive Siwalik *Sivalhippus*.

An outcome of Bernor et al.'s (2017) study was recognition that *Hippotherium* very quickly diverged from *Cormohipparion* in Central Europe and extended its range throughout Central and West Europe where *Hippotherium koenigswaldi* and *Hippotherium catalaunicum* (MN9 of Spain; Woodburne et al. 1996; Bernor et al. 1996) occur. Identification of *H. weihoense* as being a species of *Hippotherium* extends the range of this clade from Western and Central Europe to North China. Old World *Cormohipparion* on the other hand was a lower latitude clade that ranged from IndoPakistan (Wolf et al., 2013) to Turkey, North Africa and Ethiopia (Bernor et al. 2003; Bernor & Sen 2017). Central and Western Europe were warm temperate to subtropical forests and wooded grasslands in MN9 (Bernor et al. 1988), whereas the lower latitudes harbored more open "Pikermian"-like woodlands (Bernor 1983; Eronen et al. 2009; Kaya et al. 2017). The Siwaliks had wooded environments and early C4 grass present by 10 Ma., wherein equids were the first to assimilate C4 grass into their diet (Barry et al. 2002). *Cormohipparion* persisted only a short time in Pakistan before being replaced completely by *Sivalhippus nagriensis* (Wolf et al. 2013).

We believe that *Shanxihippus dermatorhinus* (Fig. 3-4) is a monospecific clade that was endemic to China (Sefve 1927; Bernor et al. 1990). *Shanxihippus* is very derived in the retraction of its snout and V-shaped premaxilla with very small, arcuate incisor arcade and the presence of a small proboscis or highly mobile upper lip. This snout morphology was likely adapted for selective feeding: feeding on leaves, forbes or grass shoots. This species is known exclusively from Baode County, Shanxi Province China and has an estimated age of ca. 7.1 - 5.7 Ma. (Kaakinen et al. 2013). Eronen et al. (2014; Tab. 4) report 6 species of hipparion from Locality 30 in the Lagrelius Collection, Uppsala (parenthetical taxonomic referrals follow revisions by Bernor et al. 1990 and Qiu et al. 1987; Sun et al. 2018): "*H". dermatorhinum* [= *S. dermatorhinus*], *"H". fossatum, "H". kreugeri* (= *H. hippidiodus*), *"H". platyodus* (= *S. platyodus*), *"H". ptychodus* (= *S. ptychodus*), and *"H". richthofeni* (= *C. forstenae*) which have C3/C4 diets. A single individual of *"H". dermatorhinum* (PMU M268 = *S. dermatorhinus* herein) has an oxygen isotope value of -8.6 and is recorded as having had a C3 diet.

Cremohipparion was a diverse clade of hipparions that ranged from as far west as Greece (*C. mediterraneum, C. proboscideum, C. matthewi, C. nikosi*), Italy and North Africa (*C. periafricanum*) through the Ukraine and Iran (*C. moldavicum* and *C. matthewi*) to IndoPakistan (*C. antelopinum*) and China (*C. forstenae* and *C. licenti*) (Bernor et al. 1996, 2013, 2016; Vlachou & Koufos 2009; Wolf et al. 2013). *Cremohipparion moldavicum* is the most primitive member of the clade, first occurring in the later Vallesian of the Ukraine (Gromova 1952; Bernor 1985; Bernor et al. 1996, 2016). *Cremohipparion* could plausibly be derived from a species of *Hippotherium* with most taxa retaining lower crowned cheek teeth and dorsoventrally extensive POFs. *Cremohipparion proboscideum* (Samos, Greece, ca. 7.4 Ma) had retracted nasals, dorsoventrally extensive POF and distinct buccinator and caninus fossae (Fig. 6A). Its retracted nasals suggest that it also had a highly mobile snout or small proboscis. *Cremohipparion licenti* had more retracted nasals than *C. proboscideum* and *Shanxihippus dermatorhinus* and in addition to buccinator, caninus and POF fossae, it had a malar fossa and the buccinator fossa was posteriorly pocketed (Fig. 6B, C). Morover, the POF had internal pits (C7B) suggesting that it had an elaborate nasal apparatus that likely included a pseudo-proboscis.

Proboscidipparion sinense was originally defined as a distinct genus by Sefve (1927) with Bernor et al. (1990) designating the Lectotype as being the skull and associated mandible in Uppsala (PMU3925; Fig. 3). Qiu et al. (1987) recognized and named a more primitive member of *Proboscidipparion, P. pater* from the early Pliocene of the Yushe Basin (ca. 5 Ma; Fig. 7). Qiu et al. (1987) and Deng (2012) have recognized *Proboscidipparion* as a subgenus of *Hipparion* s.s., whereas Bernor et al. (1996) and Bernor and Sun (2015) recognized *Proboscidipparion*'s generic distinction based on a unique suite of highly derived characters. Bernor and Sen (2017) recognized a species of *Proboscidipparion, P. heintzi* from the early Pliocene of Turkey that was similar to *P. pater* in its stage of nasal and dental evolution. Bernor et al. (2010) and Bernor and Sun (2015) recognize that *Proboscidipparion* is likely sister to Eurasian *Plesiohipparion* spp. and African *Eurygnathohippus* spp., which in turn are sister to IndoPakistan *Sivalhippus*. In the current cladistic analysis *Proboscidipparion* is

sister to *Shanxihippus* with these taxa in turn being sister to *Sivalhippus*. We believe that *Shanxihippus* could equally have been derived from the *Hippotherium* clade. Support of any of these various hypotheses require discovery of new associated cranial, mandibular, dental and postcranial material for all taxa under consideration to retest these various hypotheses

In this current contribution, we recognize three distinct clades of Old World hipparionines that underwent convergent evolution of elongate snouts, with retracted nasals and narrow arcuate premaxillary incisor arcades: *Shanxihippus dermatorhinus*, *Cremohipparion proboscideum* + *Cremohipparion licenti* and *Proboscidipparion pater* + *Proboscidipparion sinense*. None of these three lineages has a direct phylogenetic relationship with *Hipparion* s.s. whose species include: *H. prostylum, H. dietrichi, H. campbelli* and *H. hippidiodus* (Woodburne & Bernor 1980; Bernor et al. 1980, 1996, 2016). *Hipparion* s.s. had reduced to absent fossae, no nasal retraction and very slenderly built distal limb elements and was not a founding group for *Shanxihippus, Cremohipparion* or *Proboscidipparion*. All three of these clades (S+C+P) are distinguished by their evolution of retracted nasals, elongate snouts and narrow arcuate premaxillary arcades the hallmark of selective feeding. They all, to one extent or the other, independently evolved mobile snouts or pseudo-probosci. Fig. 9 presents our reconstruction of *Shanxihippus dermatorhinus*.

Conclusions

We recognize *Shanxihippus dermatorhinus* as a monospecific genus of late Miocene hipparionine horse from Locality 30, Baode County, Shanxi Province, North China. *Shanxihippus dermatorhinus* was apparently endemic to Shanxi Province, China. This species had a very elongate, anteriorly narrowing V-shaped snout with a narrow and highly arcuate incisor arcade and strongly retracted nasals. Functionally, we believe that *S. dermatorhinus* had a small pseudo-proboscis and was adapted to selective feeding. We analyse here taxa that likewise had elongate narrow snouts and retracted nasals: *Cremohipparion proboscideum, C. licenti, Proboscidipparion pater* and *P. sinense* with a significant Eurasian hipparionine and North American outgroup com-

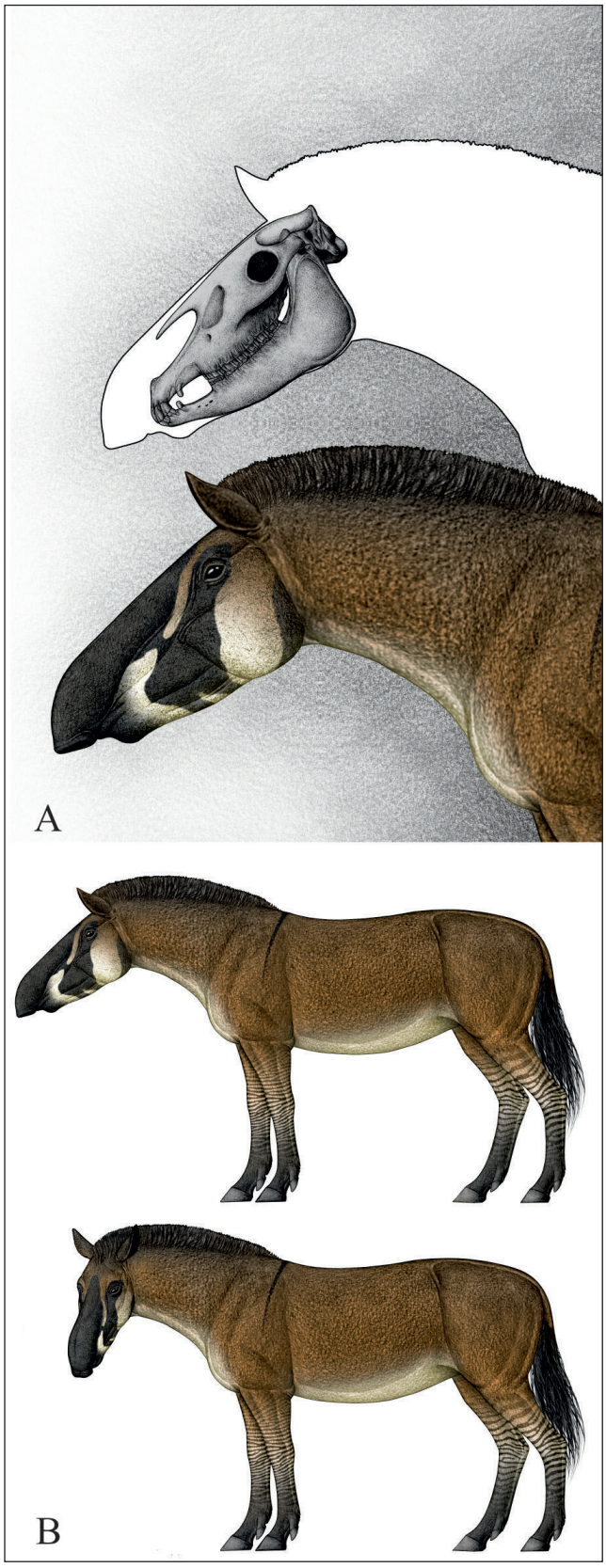

Fig. 9 - Reconstruction of *Shanxihippus dermatorhinus*. A) Skull and head reconstruction; B) standing.

parison. We believe that these three genus-level lineages (S+C+P) evolved nasal retraction and narrow premaxillary regions convergently in the late Miocene and Plio-Pleistocene as an adaptation to selective feeding. These lineages likely incorporated a significant amount of browse with graze in their diet. In the Old World, these lineages are known to geographically span from the eastern Mediterranean to China and the Indian Subcontinent, not being recorded in Central and Western Europe or Africa. They evolved within the Old World Pikermian Biome of this geographic realm (sensu Bernor 1983; Eronen et al. 2009; Solounias et al. 2010).

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Appendix 1 - tables

ID	Taxon	Quarry	SEX	BONE	SIDE	AGE (Ma)
PMUM3872	*Shanxihippus dermatorhinus*	Baode, Shanxi	3	skull		7
PMUM260	*Shanxihippus dermatorhinus*	Baode, Shanxi	3	skull		7
AMNH 127457	*Shanxihippus dermatorhinus*	Shanxi		skull with mandible		
THP14312	*Proboscidipparion pater*	Yushe, Shanxi	2	skull with mandible	lt.	4
THP20763	*Proboscidipparion pater*	Yushe, Shanxi	1	skull	rt.	4
PMUM3925	*Proboscidipparion sinense*	Mianchi, Henan		skull with mandible		
HMV 1872	*Proboscidipparion sinense*	Longdan, Gansu		skull		
THP20754	*Cremohipparion licenti*	Yushe, Shanxi		skull		
THP20764	*Cremohipparion licenti*	Yushe, Shanxi	2	skull	3	5
THP10400	*Cremohipparion licenti*	Yushe, Shanxi	3	mandible		5
AMNH117933	*Cremohipparion licenti*	Yushe, Shanxi	3	skull	lt.	5
FAM125708	*Cremohipparion licenti*	Yushe, Shanxi	3	skull		
AMNH22837B	*Cremohipparion proboscideum*			skull		
AMNH20594	*Cremohipparion proboscideum*			skull		
AMNH20672	*Cremohipparion proboscideum*			skull		
AMNH20771	*Cremohipparion proboscideum*			skull		
AMNH20772	*Cremohipparion proboscideum*			skull		
SMNSFAKrupp1895	*Cremohipparion proboscideum*			skull		

Tab. 1 - Accompanying Information on Specimens of *Shanxihippus dermatorhinus* and other Chinese hipparion species with specialized nasal apparati.

	Cooc	Hpri	Hwei	Sper	SdermT	Crprob	Crlic	Prpat	Prsin
	FAM71800	HoMEAN	IVPPV3113.3	AMNH19761	PMUM3872	SENK4709	FAM125708	THP14312dw	PMUM3925
M9	140.3	159.2	168.5	153.0		139.4	129.3	156.2	164.5
M1	110.7	140.1	134.6	116.8	114.5	132.9	114.9	118.5	127.7
M15	48.3	46.9	62.8	50.5	36.0	44.7	56.9	51.7	57.7
M30	113.5	136.6	138.8	115.7	195.9	200.9	207.4	248.9	
M31	149.4	206.9	188.5	172.0	92.2	125.1	79.1	65.0	
M32	39.7	49.0	53.6	56.2	37.3	17.8	17.6		
M33	71.3	80.5	73.2	49.2	64.3	89.1	82.3		
M35	39.3	51.5	45.1	29.1	35.4	64.1			

Tab. 2 - Measurements on variables used for Log 10 analyses (mm).

ID	PMUM3872	PMUM260	AMNH 127457
Taxon	*Shanxihippus dermatorhinum*		
M1	114.5		118.2
M2	115	98.2	102.5
M3	113		106.9
M4	90		82.5
M5	194		188.2
M6	427		411.4
M7	90	90.4	82.8
M8			66
M9			150.1
M10	49	54.8	64.2
M11	33.2	32	26.7
M12	35	35.5	33
M13	65	66.5	63
M14	36.8		35.2
M15	36		41.6
M16	73.7		
M17	115		
M18	137.4		123.2
M19	179		
M20			
M22			
M23	327.4		306.6
M24	173.2		
M25	106.5		
M26	84.7		114.3
M27	0		
M28	66	56.2	57
M29	43.2	42	49.3
M30	195.9		187.5
M31	92.2		99.4
M32	37.3	32.4	43.6
M33	64.3	58.2	66.6
M34	68.9	48.4	73.8
M35	35.4	57.8	26.5
M36	23.9	29.7	26.7
M37	53	50.2	49
M38	49.4	61.7	88.5

Tab. 3 - Standard Skull Measurements for Specimens of *Shanxihippus dermatorhinus* and other Chinese hipparion species with specialized nasal apparati (mm).

ID	THP 14312	THP 20763	PMUM 3925	HMV 1872	THP 20764	AMNH1 17933	THP 20754	FAM 125708
Taxon	*P. pater*		*P. sinense*		*C. licenti*			
M1	110.3	115.1	127.7	137				117.2
M2	125.9	124.8	145.3	135.5	105.6			106.5
M3	75.9	93.1	116.1	112.5	86			
M4	113.8	94.8	113.8	122				
M5	197.1	186.7	226.5	230				185.2
M6	437.5	422.5	501	502				411.2
M7	85.4	84.9	88.9	98.5	68.3	81.1	70.0	70.3
M8	68.9	69.1	76	83.5	56.1	65.5	57.2	59.1
M9	153.1	153.7	164.5		122.3	145.3	125.3	129.9
M10	52.6	55.7	55.2	83.5	53.4			51.7
M11	22.9	27.1	36.6		26.7		25.5	
M12	25.2	28.4	41.8		29.6		28.1	
M13	54.2	55.9	74.4		56.1		57.2	
M14	32.9	27.6	39.1					39.0
M15	45.6	37.1	57.7					54.7
M16	71	66.2	80.6	83	61.3		59.2	
M17	144.4	137.9	119.6	137.5	0			
M18	146.7	153.4	175.3		162.6		159.2	
M19	143.5	156.2	199.5		161.9		158.6	
M20	68.9							
M21								
M22	68.4	63.8	69.7					
M23	359.9	347.8	390.4	368				318.3
M24	165.3	146.8	179	190				
M25		62.2	67.5		105.5		123.7	
M26	92	98.6		112	103.6		89.1	
M27				7.5				
M28	63	58.3	65.2	67	50.8		59.8	62.0
M29	52.7	50.4		50.5	48.6		50.2	52.3
M30	245.1	227.4		272				207.9
M31	61.3	66.5		82	83.6		85.8	75.3
M32					21.7		22.8	16.0
M33					60.3		56.7	90.3
M34					61.5		53.0	
M35					39.3		43.2	39.1
M36					32.1		51.6	
M37	100.3	98.7		78	68.5		72.2	
M38					97.2		58.3	

Tab. 3 - Standard Skull Measurements for Specimens of *Shanxihippus dermatorhinus* and other Chinese hipparion species with specialized nasal apparati (mm) (continued).

ID	AMNH 22837B	AMNH 20594	AMNH 20672	AMNH 20771	AMNH 20772	SMNSFAKrupp 1895
Taxon	*Cremohipparion proboscideum*					
M1				132.8	139.2	
M2	94.9			113.0	112.3	118.5
M3	104.3					
M4						82.0
M5						321.4
M6						
M7	97.3	88.1	98.5	88.2	83.0	80.2
M8		70.3		74.2	68.2	67.2
M9		156.5		162.1	148.1	148.9
M10	60.6					71.1
M11	38.0			34.3		35.0
M12	35.2			41.3		37.5
M13	63.4	73.0	54.0	76.2	69.0	62.7
M14				42.9	42.4	
M15				57.7	49.8	
M16				76.7		72.4
M17						100.2
M18				145.2		
M19				176.0		
M20						
M21						
M22						
M23				359.2		
M24						
M25						
M26				101.3		
M27						
M28			51.9	59.7		
M29		49.1		51.7		
M30						
M31						173.9
M32	19.4	19.5	27.1	27.9		28.0
M33	70.8	91.8	68.7			70.9
M34	74.3			71.8		78.4
M35	41.7	46.6	51.2			52.2
M36	12.7	16.8	14.8	16.6	17.1	23.4
M37	36.6		34.9	48.1	50.7	
M38		78.1	54.3	88.7		66.1

Tab. 3 - Standard Skull Measurements for Specimens of *Shanxihippus dermatorhinus* and other Chinese hipparion species with specialized nasal apparati (mm) (continued).

ID	AMNH 127457	THP14312	PMUM3925
Taxon	*S. dermatorhinus*	*P. pater*	*P. sinense*
M1		421.5	470
M2	105.8	109.7	126.8
M3	78.6	82.9	88.1
M4		70.9	81.7
M5		153.9	171.6
M6		117.9	134.1
M7	44.5	49.8	57.4
M8			215.5
M9			206
M10	98		108.3
M11	69.4		87.3
M12	44.5	51.7	66.4
M13	75.9	81	103.8
M14	25.6	30.1	36

Tab. 4 - Standard Mandible Measurements for Specimens of *Shanxihippus dermatorhinus* and other Chinese hipparion species with specialized nasal apparati (mm).

ID	PMUM3872		PMUM260					AMNH 127457									
Taxon	*Shanxihippus dermatorhinum*																
Tooth	M1	M2	M1	P2	P3	P4	M1	I1	I2	I3	C	P2	P3	P4	M1	M2	M3
M1	26.5	24	27.4	35.5	26.6	26.8	23.1	17.1	17.4	17.6	5.7	31.7	25.9	25.8	23.1	23.7	21.7
M2																	
M3	24.3	22.8	21.9	25.3	26.7		24.5	9.7	7.5	6.4	4.8	23.2	25	25.3	22.7	20.9	16.4
M4																	
M5																	
M6												4	5	3	3	3	3
M7												5	5	4	6	4	4
M8												3	4	3	4	4	
M9												5	2	3	2	2	
M10	7.6		7.9	8.4	9.1	9.2	8.3					6.9	7.8	8.8	7.6	7.4	7.4
M11	3.6		3.2	5.2	4.6	4.6	4.8					4.7	3.8	4.1	3.6	3.2	2.3

Tab. 5 - Standard Maxillary Cheek Tooth Measurements for Specimens of *Shanxihippus dermatorhinus* and other Chinese hipparion species with specialized nasal apparati (mm).

ID	THP14312									THP20763								
Taxon	*Proboscidipparion pater*																	
Tooth	I1	I2	I3	P2	P3	P4	M1	M2	M3	I1	I2	I3	P2	P3	P4	M1	M2	M3
M1	15.9	16.5	15.5	34.6	25.7	24.4	22.9	23.4	19.8	14	16.6	16.8	34.5	25.6	24.5	24.1	24.1	21.9
M2																		
M3	9	7.3	6.6	22.8	25.2	23.5	22.4	20.6	15.5	9.7	9.2	7.4	22.4	23.3	22.7	23.4	20.1	11.4
M4																		
M5													49.4					
M6				4.0	4.0	7.0	7.0	5.0	2.0				4	5	5	8	13	4
M7				5.0	4.0		4.0						5	5	4	5	6	3
M8				5.0	3.0		5.0	5.0					4	3	3	6	4	2
M9				2.0	2.0			4.0					2	2	1	4	3	3
M10				6.2	5.7	7.9	7.7	6.2	6.3				8.9	6.5	6.8	6.6	6	7.1
M11				4.4	5.6	4.3	4.8	5.2	2.4				3.9	4.1	3.8	3.7	3.5	3.3

Tab. 5 - Standard Maxillary Cheek Tooth Measurements for Specimens of *Shanxihippus dermatorhinus* and other Chinese hipparion species with specialized nasal apparati (mm) (continued).

ID	PMUM3925						HMV1872					
Taxon	*Proboscidipparion sinense*											
Tooth	P2	P3	P4	M1	M2	M3	P2	P3	P4	M1	M2	M3
M1	40	30	24.5	23.5	24		40.5	30	28.4	29	26.8	
M2												
M3	25	25	25	25	23		24.6	24.1	21	22	19.6	
M4												
M5												
M6												
M7												
M8												
M9												
M10	8	10.8	11	9.7	10		10.8	8.2	9.7	8.5	10	
M11		6.5	6		5.5			6.9	5.2	3.8	3.5	

Tab. 5 - Standard Maxillary Cheek Tooth Measurements for Specimens of *Shanxihippus dermatorhinus* and other Chinese hipparion species with specialized nasal apparati (mm) (continued).

ID	THP20764						AMNH117933					
Taxon	*Cremohipparion licenti*											
Tooth	P2	P3	P4	M1	M2	M3	P2	P3	P4	M1	M2	M3
M1	28.1	20	20	18	17.5	19.5	34.5	24.6	23.2	21	21.8	21.7
M2												
M3	20.4	20.9	21.3	20.9	20.1	18.9	21.6	22	20.5	20.4	19.6	18.2
M4												
M5							30.3					
M6	3	1	1	1		1		1	2	1	3	
M7	5	4	6	4	4	4	2	4	2	4	3	
M8	1	2	1	2	2	4	1	1	2	3	2	
M9						1	1		1			
M10	5.6	5.2	5.7	5.4	5.7	4.9	6.5	5.5	5.9	6.3	5.6	5.9
M11	4.5	4.2	4.1	3.7	4.6	2.8	4.4	3.8	3.4	3.8	3.5	3.1

Tab. 5 - Standard Maxillary Cheek Tooth Measurements for Specimens of *Shanxihippus dermatorhinus* and other Chinese hipparion species with specialized nasal apparati (mm) (continued).

ID	THP20754						FAM125708									
Taxon	*Cremohipparion licenti*															
Tooth	P2	P3	P4	M1	M2	M3	I1	I2	I3	C	P2	P3	P4	M1	M2	M3
M1	22.6	21.2	21	18	18.5	20.7	10.5	9.2	10.9	10.8	27.3	20.4	20.5	18.2	19.7	23.6
M2																
M3	20	21.2	21.6	20.2	20.5	17.6				6.8	21.7	24.5	23.6	22.6	21.2	19.4
M4																
M5																
M6	3										1.0		1.0			1.0
M7	6	3	5	4	4	5					1.0		4.0	4.0	3.0	4.0
M8	1		1	1	2	4					1.0					
M9			1			1										
M10	5.6	5.6	5.9	5.5	5.5	4.5						6.0	6.9	5.4	6.0	6.2
M11	4.4	4.7	4.3	4	3.8	2.2					5.8	5.1	4.9	4.3	3.6	3.8

Tab. 5 - Standard Maxillary Cheek Tooth Measurements for Specimens of *Shanxihippus dermatorhinus* and other Chinese hipparion species with specialized nasal apparati (mm) (continued).

ID	AMNH22837B			AMNH20594						AMNH20635						
Taxon	*Cremohipparion proboscideum*															
Tooth	DP2	DP3	DP4	P2	P3	P4	M1	M2	M3	DP1	P2	P3	P4	M1	M2	M3
M1	37.5	29.5	28.7	35.5	27.1	25.8	22.8	24.3	25	10.4	38.1	25.1	25.4	23.2	24.2	25.1
M2				0	0	0	0	0	0							
M3	21.8	22.1	19.2	26.2	26.7	27.9	26.1	24.4	22.3	7.9	25.4	25.7	26.4	24.2	22.9	20.7
M4				0	0	0	0	0	0							
M5	17.4	16.7	17.7	0	0	0	0	0	0							
M6				0.0	0.0	0.0	0.0	0.0	0.0		4.0	4.0	5.0	4.0	2.0	1.0
M7				0	0	0	0	0	0		6	8	8	8	5	6
M8				0	0.0	0	0	0	0		5	6	4	6	5	5
M9				0	0	0	0	0	0		1	1	1	1	2	1
M10	5.5	5.9	6.4	8.3	8.0	7.1	7.1	6.5	7.8		7.6	7.5	8.5	8.0	7.9	8.0
M11	3.7	3.6	4	5.6	6	5.4	4.8	4.5	4.1		5.3	5.3	6.1	5.1	5.2	4.3

Tab. 5 - Standard Maxillary Cheek Tooth Measurements for Specimens of *Shanxihippus dermatorhinus* and other Chinese hipparion species with specialized nasal apparati (mm) (continued).

ID	AMNH20672				AMNH20771				
Taxon	*Cremohipparion proboscideum*								
Tooth	DP2	DP3	DP4	I1	P2	P3	P4	M1	M2
M1	38.3	28.7	29.7	18.4	32.1	27.9	26.5	26.1	25.9
M2					0	0	0	0	0
M3	21.5	21.5	20.8		22.4	25.2	24	22.2	20.3
M4					0	0	0	0	0
M5	16.8	16.2	18		0	0	0	0	0
M6					0.0	0.0	0.0	0.0	0.0
M7					0	0	0	0	0
M8					0	0	0.0	0.0	0
M9					0	0	0	0	0
M10	6.1	5.2	5.6		5.8	7.0	0.0	6.3	5.2
M11	4.2	4.5	3.8		4.7	5.1	0	4.6	4.1

Tab. 5 - Standard Maxillary Cheek Tooth Measurements for Specimens of *Shanxihippus dermatorhinus* and other Chinese hipparion species with specialized nasal apparati (mm) (continued).

ID	AMNH20772										SMNSFAKrupp1895					
Taxon	*Cremohipparion proboscideum*															
Tooth	I1	I2	I3	C	P2	P3	P4	M1	M2	M3	P2	P3	P4	M1	M2	M3
M1	14.9	16.7	18.1	4.3	34.2	24.8	24.8	21.9	22.1	25.6	34.3	25	22.9	20.9	21.3	23.8
M2	0	0	0	0	0	0	0	0	0	0						
M3	9.9	9	7.4	4.7	23.0	26.8	25	25.7	23.4	20.8	23.8	26.2	25.6	23.9	24	21.9
M4					0	0	0	0	0	0						
M5					0	0	0	0	0	0	9.1	8.4	8.8	7.8	8.9	11.6
M6					0	0	0	0.0	0	0	0	0	0	0	0	0
M7					0	0	0	0	0	0	2	0	3	0	3	2
M8					0	0	0	0.0	0	0	0	0	0	0	0	0
M9					0	0	0	0	0	0	0	0	0	0	0	1
M10					7.2	7.2	7.9	8.0	7.9	8.1			7.7			
M11					5.8	6.1	6.1	6.1	5.8	4.8			6.2			

Tab. 5 -Standard Maxillary Cheek Tooth Measurements for Specimens of *Shanxihippus dermatorhinus* and other Chinese hipparion species with specialized nasal apparati (mm) (continued).

ID	AMNH127457					THP14312									THP10400				
Taxon	*Shanxihippus dermatorhinus*					*Proboscidipparion pater*									*Cremohipparion licenti*				
Tooth	p2	p3	p4	m2	m3	i1	i2	i3	p2	p3	p4	m1	m2	m3	p2	p3	p4	m1	m2
M1	29	24.3	25.8	23.6	23.2	15.5	16.2	18.6	30.9	27.8	25.6	25.3	24.3	22.8	23	21.8	20.4	22.9	20.6
M2																			
M3						12.1	9.1	9.1	7.9	16		14.5	12.7	10	11.2	13.1	13.4	12.4	11.1
M4									10.2	10.2	14.1	8.1	8	8.6	6.5	6.7	5.9	6.1	5.8
M5									15.3	14.1	13.9	10.6	12.3	9.1	10.5	11.2	10.8	8.3	8.4
M6	12.3	14.1	13.7	10.5	8.8				13.4	15	14.3	12.5	11.5	9.5	11.2	11.9	11.8	8.2	8.1
M7																			
M8	9.6	11.4	11.4	9.3	8.6				9.9	14.3		11.4	10.6	7.8	9.7	11.5	11.4	10.7	9.9
M9	11.5	12.2	10.6	9.9	8.1				11.9	13.3	10.9	10	9.6	7.3	11.8	12.3	10.6	9.2	9

Tab. 6 - Standard Mandibular Tooth Measurements for Specimens of *Shanxihippus dermatorhinus* and other Chinese hipparion species with specialized nasal apparati (mm).

SPECIMEN NO	TAXON	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	C14	C15	C16	C17	C18	C19
	Parahippus leonensis	A	C	A	A	D	C	A	BC	B	A	A	A	A	A	A	?	A	B	A
	Merychippus insignis	A	C	A	A	C	B	A	B	A	A	A	A	A	A	A	?	A	AB	A
	C. quinni	B	C	?	A	A	A	A	A	A	B	B	A	A	A	B	?	A	B	?
FAM71800	*C. occidentale*	C	C	B	D	A	A	A	A	A	B	B	A	A	A	B	A	B	B	B
NHMW4249	*H. primigenium*	C	C	B	D	A	A	A	A	A	B	B	A	A	A	B	A	AB	B	B
SMNK&HLMD Mean	*H. primigenium*	C	C	B	D	A	A	A	A	A	B	B	A	A	A	B	A	AB	B	B
IVPPV3113.3	*H. weihoense*	C	C	B	E	A	A	A	A	A	B	B	A	A	A	C	A	B	B	B
AMNH19761	*S. perimensis*	F	C	B	F	C	B	A	A	A	B	B	A	A	A	C	A	B	B	B
PMUM3872	*S. dermatorhinus*	C	C	B	D	B	B	A	A	A	B	B	A	A	A	F	B	B	B	B
AMNH 41 L310	*S. dermatorhinus*	C	C	B	D	B	B	A	A	A	B	B	A	A	A	F	B	B	B	B
SENK4709	*C. proboscideum*	B	C	B	D	B	A	A	A	A	B	B	A	B	A	E	A	B	A	B
FAM125708	*C. licenti*	B	C	B	D	B	A	B	A	A	B	B	B	B	B	G	A	B	A	B
THP14312	*P. pater*	G	C	B	I	E	D	A	E	B	C	B	A	A	A	G	C	B	B	B
PMUM3925	*P. sinense*	G	C	B	I	E	D	A	E	B	C	B	A	A	A	H	C	B	B	B

Tab. 7 - Hipparionine Character States.

SPECIMEN NO	TAXON	C20	C21	C22	C23	C24	C25	C26	C27	C28	C29	C30	C31	C32	C33	C34	C35	C36
	Parahippus leonensis	A	C	AB	A	D	B	A	B	A	A	A	A	B	A	?	?	A
	Merychippus insignis	A	BC	AB	A	B	AB	A	B	B	AB	B	?	A	?	?	?	A
	C. quinni	C	B	AB	B	AB	B	B	B	B	B	B	B	A	?	?	?	A
FAM71800	*C. occidentale*	C	B	AB	B	AB	B	D	A	B	BC	B	B	A	A	A	A	A
NHMW4249	*H. primigenium*	C	A	AB	B	AC	B	E	A	B	BC	B	B	A	?	?	?	?
SMNK&HLMD Mean	*H. primigenium*	C	A	AB	B	AC	B	E	A	B	BC	B	B	A	A	A	A	A
IVPPV3113.3	*H. weihoense*	C	A	B	B	A	B	E	A	B	C	B	B	A	?	?	?	?
AMNH19761	*S. perimensis*	D	A	B	B	A	B	E	A	B	C	B	B	A	A	A	A	?
PMUM3872	*S. dermatorhinus*	CD	A	B	B	AB	B	J	B	B	C	B	B	A	?	?	?	?
AMNH 41 L310	*S. dermatorhinus*	CD	A	AB	B	AB	B	J	B	B	BC	B	B	A	A	A	A	AB
SENK4709	*C. proboscideum*	C	C	B	B	A	CD	CD	B	B	C	B	B	A	?	?	?	?
FAM125708	*C. licenti*	C	C	B	B	B	CD	E	B	B	C	B	B	B	?	?	?	?
THP14312	*P. pater*	D	A	B	B	A	B	E	A	B	C	B	B	A	A	A	A	?
PMUM3925	*P. sinense*	E	A	B	B	C	B	I	A	B	C	B	B	A	A	A	A	A

Tab. 7 - Hipparionine Character States (continued).

SPECIMEN NO	TAXON	C37	C38	C39	C40	C41	C42	C43	C44	C45	C46	C47	C48	C49	C50	C51	C52	C53
	Parahippus leonensis	A	A	B	A	B	AB	B	C	B	?	B	A	A	A	A	A	A
	Merychippus insignis	A	A	?	A	?	?	?	C	B	?	?	A	A	A	A	?	A
	C. quinni	A	A	?	A	?	A	?	B	?	?	?	A	B	B	B	?	A
FAM71800	*C. occidentale*	A	?	?	?	?	?	?	?	B	C	?	A	AC	?	?	A	A
NHMW4249	*H. primigenium*	?	?	?	?	?	?	?	?	?	?	B	?	?	?	?	?	?
SMNK&HLMD Mean	*H. primigenium*	A	AE	AB	E	AB	AB	AB	BC	A	C	AB	A	BC	B	B	A	A
IVPPV3113.3	*H. weihoense*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
AMNH19761	*S. perimensis*	A	AE	B	E	B	AB	AB	BC	C	C	AB	A	BC	B	B	A	A
PMUM3872	*S. dermatorhinus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
AMNH 41 L310	*S. dermatorhinus*	A	AC	AB	AC	B	A	AB	BC	AB	D	B	A	BC	A	A	A	A
SENK4709	*C. proboscideum*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
FAM125708	*C. licenti*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
THP14312	*P. pater*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
PMUM3925	*P. sinense*	C	C	B	C	B	A	AB	C	B	F	B	D	D	A	A	A	A

Tab. 7 - Hipparionine Character States (continued).

APPENDIX 2 - TABLE 7 LEGEND: HIPPARIONINE CHARACTER STATES (BERNOR ET AL., 1990; 2017)

1) Relationship of lacrimal to the preorbital fossa: A = lacrimal large, rectangularly shaped, invades medial wall and posterior aspect of preorbital fossa; B = lacrimal reduced in size, slightly invades or touches posterior border of preorbital fossa; C = preorbital bar (POB) long with the anterior edge of the lacrimal placed more than half the distance from the anterior orbital rim to the posterior rim of the fossa; D = POB reduced slightly in length but with the anterior edge of the lacrimal placed still more than 1/2 the distance from the anterior orbital rim to the posterior rim of the fossa; E = POB vestigial, but lacrimal as in D; F = POB very long with anterior edge of lacrimal placed less than 1/2 the distance from the anterior orbital rim to the posterior rim of the fossa; H = POB absent; G = POB absent;
2) Nasolacrimal fossa: A = POF large, ovoid shape and separated by a distinct medially placed, dorsoventrally oriented ridge, dividing POF into equal anterior (nasomaxillary) and posterior (nasolacrimal) fossae; B = nasomaxillary fossa sharply reduced compared to nasolacrimal fossa; C = nasomaxillary fossa absent (lost), leaving only nasolacrimal portion (when a POF is present).
3) Orbital surface of lacrimal bone: A = with foramen; B = reduced foramen.
4) Preorbital fossa morphology: A = large, ovoid shape, anteroposteriorly oriented; B = POF truncated anteriorly; C = POF further truncated, dorsoventrally restricted at anterior limit; (note CSk A-C are pre-Old World hipparionine characters); D = subtriangular shaped and anteroventrally oriented; E = subtriangularly shaped and anteroposteriorly oriented; F = egg-shaped and anteroposteriorly oriented; G = C-shaped and anteroposteriorly oriented; H = vestigial but with a C-shaped or egg-shaped outline; I = vestigial without C-shape outline, or absent; J = elongate, anteroposteriorly oriented; K = small, rounded structure; L = posterior rim straight, with non-oriented medial depression; M = posteriorly, POF very extensive dorsoventrally.
5) Fossa posterior pocketing: A = deeply pocketed, greater than 15 mm in deepest place; B = pocketing reduced, moderate to slight depth, less than 15 mm; C = not pocketed but with a posterior rim; D = absent, no rim but a remnant depression; E = absent.
6) Fossa medial depth; A = deep, greater than 15 mm. in deepest place; B = moderate depth, 10-15 mm in deepest place; C = shallow depth, less than 10 mm in deepest place; D = absent.
7) Preorbital fossa medial wall morphology: A = without internal pits; B = with internal pits.
8) Fossa peripheral border outline: A = strongly delineated around entire periphery; B = moderately delineated around periphery; C = weakly defined around periphery; D = absent with a remnant depression; E = absent, no remnant depression.
9) Anterior rim morphology: A = present; B = absent.
10) Placement of infraorbital foramen: A = placed distinctly ventral to approximately 1/2 the distance between the preorbital fossa's anteriormost and posteriormost extent (pre- Old World hipparionine condition); B = inferior to, or encroaching upon anteroventral border of the preorbital fossa; C = placed high on maxilla near orbit.
11) Confluence of buccinator and canine fossae: A = present (pre-Old World hipparionine condition); B = absent, buccinator fossa is distinctly delimited.
12) Buccinator fossa: A = not pocketed posteriorly; B = pocketed posteriorly.
13) Caninus (= intermediate) fossa: A = absent; B = present.
14) Malar fossa: A = absent; B = present.
15) Nasal notch position: A = at posterior border of canine or slightly posterior to canine border; B = approximately half the distance between canine and P2; C = at or near the anterior border of P2; D = above P2; E = above P3; F = above P4; G = above Ml; H = posterior to Ml.
16) Shape of premaxilla: A= straight; B = V-shaped; C = dorsally convex in incisor region.
17) Presence of dP1 (16U) or dP1, (16L): A = persistent and functional; B = reduced and non-functional; C = absent.
18) dP2 anterostyle: A = short; B = elongate.
19) Curvature of maxillary cheek teeth: A = very curved; B = moderately curved; C = straight.
20) Maximum cheek tooth crown height: A = < 30 mm; B = 30 - 40 mm; C = 40 - 59 mm; D = 60 - 65 mm; E = 66-74; E = 75+ maximum crown height.
21) Maxillary cheek tooth fossette ornamentation: A = complex, with several deeply amplified plications; B = moderately complex with fewer, more shortly amplified, thinly banded plications; C = simple complexity with few, shortly amplified plications; D = generally no plis; E = very complex.
22) Confluence (linkage) of pre- and postfosstte opposing borders: A = linked; B = separate.
23) Posterior wall of postfossette: A = may not be distinct; B = always distinct.
24) Pli caballin morphology: A = double; B = single or occasionally poorly defined double; C = complex; D = plis not well formed.
25) Hypoglyph: A = hypocone frequently encircled by hypo- glyph; B = deeply incised, infrequently encircled hypocone; C = moderately deeply incised; D = shallowly incised.
26) Protocone shape: A = round q-shape; B = oval q-shape; C = oval; D = elongate-oval; E = lingually flattened-labially rounded; F = compressed or ovate; G = rounded; H = triangular; I = triangular-elongate; J = lenticular; K = triangular with rounded corners.
27) Protocone flattened: A = yes; B = no
28) Isolation of protocone: A = connected to protoloph; B = isolated from protoloph.
29) Protoconal spur: A = elongate, strongly present; B = reduced; C = absent.
30) Premolar protocone/hypocone alignment (pre- Old World hipparionine condition): A = anteroposteriorly aligned; B = protocone more lingually placed.
31) Molar protocone/hypocone alignment (pre- Old World hipparionine condition):: A = anteroposteriorly aligned; B = protocone more lingually placed.
32) P2 anterostyle U/anterostylid L: A = elongate; B = short and rounded.
33) Mandibular incisor morphology: A = not grooved; B = grooved.
34) Mandibular incisor curvature: A = curved; B = straight.
35) I3 lateral aspect: A = elongate, not labiolingually constricted; B = very elongate, labiolingually constricted distally; C = atrophied.
36) Premolar metaconid: A = rounded; B = elongated; C = angular on distal surface; D = irregular shaped; E = square shaped; F = pointed.
37) Molar metaconid: A = rounded; B = elongated; C = angular on distal surface; D = irregular shaped; E = square shaped; F = pointed.
38) Premolar metastylid:: A = rounded; B = elongate; C = angular on mesial surface; D = irregular shaped; E = square shaped; F = pointed.
39) Premolar metastylid spur: A = present; B = absent
40) Molar metastylid: A = rounded; B = elongate; C = angular on mesial surface; D = irregular shaped; E = square shaped; F = pointed.
41) Molar metastylid spur: A = present; B = absent
42) Premolar ectoflexid: A = does not separate metaconid and metastylid; B = separates metaconid and metastylid.
43) Molar ectoflexid: A = does not separate metaconid and metastylid; B = separates metaconid and metastylid; C = conver-

ges with preflexid and postflexid to abutt against metaconid and metastylid.

44) Pli caballinid: A = complex; B = rudimentary or single; C = absent.

45) Protostylid: A = present on occlusal surface often as an enclosed enamel ring; B = absent on occlusal surface, but may be on side of crown buried in cement; C = strong, columnar; D = a loop; E = a small, poorly developed loop; F = a small, pointed projection continuous with the buccal cingulum.

46) Protostylid orientation: A = courses obliquely to anterior surface of tooth; B = less oblique coursing, placed on anterior surface of tooth; C = vertically placed, lies flush with protoconid enamel band; D = vertically placed, lying lateral to protoconid band; E = open loop extending posterolabially; F = absent.

47) Ectostylids: A = present; B = absent.

48) Premolar linguaflexid: A = shallow; B = deeper, V-shaped; C = shallow U-shaped; D = deep, broad U-shape; E = very broad and deep.

49) Molar linguaflexid: A = shallow; B = V-shaped; C = shallow U-shaped; D = deep, broad U-shape; E = very broad and deep.

50) Preflexid morphology: A = simple margins; B = complex margins; C = very complex.

51) Postflexid morphology: A = simple margins; B = complex margins; C = very complex.

52) Postflexid invades metaconid/metastylid junction by anteriormost portion bending sharply lingually: A = no; B = yes.

53) Protoconid enamel band morphology: A = rounded; B = flattened.