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# *SIVALHIPPUS PTYCHODUS* AND *SIVALHIPPUS PLATYODUS* (PERISSODACTYLA, MAMMALIA) FROM THE LATE MIOCENE OF CHINA

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*Keywords*: *Sivalhippus ptychodus; Sivalhippus platyodus;* late Miocene; Evolution; Biogeography.

*Abstract.* Herein, the authors report on skulls, mandibles and postcranial specimens of two species of Chinese *Sivalhippus, S. ptychodus* and *S. platyodus*. We frame our description and analyses within the context of newly described characters of the cheek teeth of *Hippotherium* from the Pannonian C of the Vienna Basin, the oldest and most primitive Old World hipparions. Our report includes original skull, mandibular and limited postcranial material of *Sivalhippus ptychodus* and skulls and dentitions of *Sivalhippus platyodus* from the Paleontological Museum of Uppsala (PMU, Uppsala, Sweden), the American Museum of Natural History (AMNH, New York, USA) and the Licent Collection in Tianjin Natural History Museum (Tianjin, China). The skull, maxillary and mandibular material we attribute to *Sivalhippus ptychodus* and *Sivalhippus platyodus* exhibit some primitive features for Old World hipparions and synapamorphies of the face and dentition that unite it with the *Sivalhippus* clade. Our analysis shows that *S. ptychodus* and *S. platyodus* differ significantly from the *Cormohipparion occidentale – Hippotherium primigenium* clade. Species belonging to the *Sivalhippus* clade are found in IndoPakistan (*S. nagriensis, S. theobaldi, S. perimensis* and *S. anwari*), Libya and Kenya (*S. turkanensis*) and Uganda (*S. macrodon*). We hypothesize that the *Sivalhippus* clade originated in South Asia where it is earliest represented by *Sivalhipus nagriensis,* ca. 10.4 Ma and underwent range extension into Africa and China circa 9-7 Ma.

## INTRODUCTION

*Sivalhippus* is a derived lineage of Eurasian and African hipparion horses (Bernor & Hussain 1985; Wolf et al. 2013). This genus first appears in IndoPakistan and appeared later in the late Miocene in China and Africa. Lydekker (1877a) originally erected the genus *Sivalhippus* and the taxon has been recognized by a number of authors since then (Lydekker 1877b, 1882, 1885; Pilgrim 1910, 1913; Matthew 1929; Colbert 1935; Forsten 1968; Hussain 1971; Skinner & MacFadden 1977; MacFadden & Bakr 1979; MacFadden & Woodburne 1982; Hussain & Bernor 1984; Bernor & Hussain 1985; Bernor et al. 2010; Wolf et al. 2013; Sun 2013; Bernor & Sun 2015). Wolf et al. (2013) recognized that *Sivalhippus* is a clade in IndoPakistan (*S. nagriensis, S. theobaldi, S. perimensis* and *S. anwari*), Libya and Kenya (*S. turkanensis*) and Uganda (*S. macrodon*). However, two Chinese taxa have been referred to the *Sivalhippus* group and are in need of description within a contemporary morphological and evolutionary context: *Sivalhippus platyodus* and *Sivalhippus ptychodus* (following Bernor et al. 1990; Bernor & Lipcomb 1991; Wolf et al. 2013). Although some authors such as Bernor et al. (1990) suggested a possible affinity of these Chinese taxa with *Sivalhippus* (sensu Bernor et al. 1990; Bernor & Lipcomb 1991; Wolf et al. 2013), their formal recognition, characterization and evolutionary relationships have not occurred until this contribution.

We identify four skulls and two fragmental mandibles of *Sivalhippus ptychodus* housed in Museum of Evolution of Uppsala University, Uppsala, Sweden (PMU). In addition, we have recently discovered a mandible from Qingyang, China in the Licent Collection housed in Tianjin Natural History Museum. The Qingyang area was discovered by the

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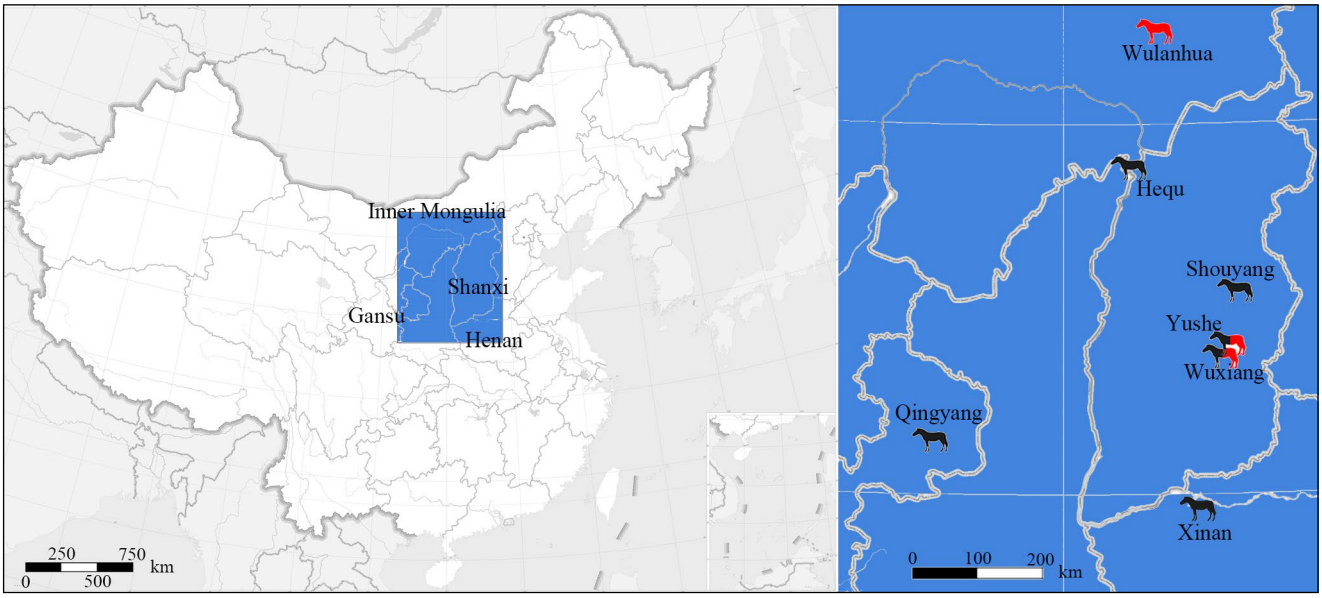


Fig. 1 - Distribution of *S. ptychodus* (black horse) and *S. platyodus* (red horse) in China. Mixed color shows coexistence.

French Jesuit priest, Emile Licent (Figure 1 – Locator Map). As a missionary, Licent was sent to China in 1914 to initiate natural science investigations (Qiu et al. 2013). Early on, Licent worked in the Qingyang area, eastern Gansu Province, and reported his discoveries in the French newspaper La Politique de Peking (August, 1920). In October 1921, Licent selected some well-preserved and representative specimens, and sent them to the Museum National d'Histoire Naturelle, Paris. Based on this material, Teilhard de Chardin (1922) submitted a report to the Geological Society of France under the title: "Sur une faune de mammiferes Pontiens provenant de la Chine septentrionale". Nevertheless, Licent deposited several Qingyang specimens in the Musée Hoang-ho Pai-ho de Tientsin (now Tianjin Natural History Museum, THP). These specimens include hyena material studied by Qiu et al. (1979), giraffe material (lacking any systematic report) and hipparion specimens most of which have been studied by Qiu et al. (1987). The mandible described in this manuscript has not previously been reported or described. Its dental characters such as small size, short p2 and triangular metaconid and metastylid are very similar as *S. ptychodus*.

We also recently have recognized specimens of *Sivalhippus ptychodus* in the American Museum of Natural History, including a complete skull and associated jaw. It was identified as "*Hipparion*" cf. *platyodus* by Bernor et al. (1990). However, its facial morphology reveals its identity as *Sivalhippus ptychodus* and is the best preserved specimen of this species including complete skull and mandible. Material that we recognize as belonging to *Sivalhippus platyodus* include one skull and associated mandible in Uppsala and one skull in Tianjin. Our report leads us to provide the morphological distinction of *S. ptychodus* and *S. platyodus* and their geographic and chronologic ranges in China (Fig. 1), and their evolutionary and biogeographic relationships with Indo-Pakistan and African species of *Sivalhippus*.

## 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, 1997). The taxon *Hipparion* has been applied in a variety of ways by different authors. We utilize the following definitions in this work:

Hipparionini (or, the common name hipparionines) - a tribe of Equidae with an isolated protocone on maxillary premolar and molar teeth and, as far as known, tridactyl feet. Bernor et al. (1996, 2010, 2016) has recognized 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.

| ID | Taxon | Quarry | SEX | BONE | SIDE | AGE (Ma) |
|---|---|---|---|---|---|---|
| PMUM347 | *S. ptychodus* Lectotype | Wuxiang, Shanxi | 3 | skull | lt. | 7-6.5 |
| PMUM350 | *S. ptychodus* | Hequ, Shanxi | 3 | skull | lt. | |
| PMUM593 | *S. ptychodus* | Hequ, Shanxi | 3 | skull | lt. | |
| PMUM3684 | *S. ptychodus* | Yushe, Shanxi | Male | skull | lt. | 6.5 |
| AMNH143267 | *S. ptychodus* | Shouyang, Shanxi | Male | skull with mandible | lt. | |
| THP01839 | *S. ptychodus* | Qingyang, Gansu | 3 | mandible | lt. | 7 |
| PMUM353 | *S. ptychodus* | Wuxiang, Shanxi | Male | mandible | lt. | 7-6.5 |
| PMUM356 | *S. ptychodus* | Xinan, Henan | 3 | mandible | rt. | |
| PMUM3691 | *S. platyodus* Lectotype | Wuxiang, Shanxi | Male | skull with mandible | lt. | 7-6.5 |
| THP22708 | *S. platyodus* | Yushe, Shanxi | Female | skull | lt. | 6.5 |

Tab. 1 - Accompanying information on specimens of Chinese species of *Sivalhippus*.

(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 multi-species 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 *Sivalhippus ptychodus* and *Sivalhippus platyodus* are listed in Tab. 1 with accompanying information on their geographic location and chronologic age. Tabs 2-6 list standard measurements for specimens (after Bernor et al. 1997) referred to these two Chinese species of *Sivalhippus*: Tab. 2, skulls; Tab. 3, maxillary dentition; Tab. 4, mandibles; Tab. 5, mandibular dentitions; Tab. 6, metapodial measurements. Tab. 7 provides measurements on key features of *Sivalhippus* skulls used in our following analyses. We cite these measurements in our description of skulls.

## Character State Distribution

Tab. 8 summarizes the characters state distribution of *Sivalhippus ptychodus* and *Sivalhippus platyodus* updated from Bernor et al. (1990) including new character state attributes from Bernor et al. (2017). The new additional characters of the maxillary and mandibular cheek teeth follow the 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 as intermediate (i.e., a/ is intermediate between states a and b). When variable, we record 2 or more states without a / but use of an intervening comma (, - i.e. 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.

| ID | PMUM 347 | PMUM 3684 | PMUM 350 | PMUM 593 | AMNH 143267 | PMUM 3691 | THP 22708 |
|---|---|---|---|---|---|---|---|
| Taxon | | | *S. ptychodus* | | | *S. platyodus* | |
| M1 | | 102.5 | | | 108.8 | 98.8 | 97.0 |
| M2 | 91.2 | 106.8 | 99.6 | 111.9 | 101.3 | 111.7 | 86.8 |
| M3 | 121.0 | | 97.0 | | | 84.6 | |
| M4 | | | | | | | |
| M5 | | | | | 174.8 | | |
| M6 | | | | | 379.9 | | |
| M7 | 73.0 | 76.3 | 77.2 | 75.3 | 73.6 | 82.5 | 77.6 |
| M8 | 62.2 | 62.8 | | 67.1 | 60.4 | 66.5 | 64.7 |
| M9 | 134.8 | 136.8 | | 142.2 | 133.8 | 149.2 | 140.0 |
| M10 | 70.7 | 61.0 | 56.5 | 65.8 | | 51.6 | |
| M11 | 32.8 | 38.8 | 29.5 | 22.0 | 31.9 | 29.7 | |
| M12 | 35.7 | 38.1 | 31.2 | 31.0 | 29.1 | 31.8 | 37.3 |
| M13 | 68.6 | 66.0 | 53.4 | 28.3 | | 56.8 | 57.6 |
| M14 | 42.0 | 34.0 | | | 26.8 | 33.5 | 35.3 |
| M15 | | 44.7 | | | 33.3 | 45.7 | 47.2 |
| M16 | 78.0 | | | | | 77.5 | |
| M17 | 121.0 | | | | | | |
| M18 | 148.0 | | 117.0 | 63.0 | | 142.0 | |
| M19 | 181.0 | | 146.0 | | | 171.0 | |
| M20 | | | | | | | |
| M21 | | | | | | | |
| M22 | | | | | 62.2 | | |
| M23 | | 284.8 | | | 295.6 | 292.4 | 218.3 |
| M24 | | | | | 163.2 | | |
| M25 | 89.0 | 80.7 | 65.4 | 89.0 | 95.5 | 78.1 | 77.2 |
| M26 | 105.0 | | 74.0 | | 93.6 | 80.7 | |
| M27 | | | | | | | |
| M28 | 56.1 | | 54.6 | 58.1 | 59.0 | 55.5 | |
| M29 | 45.8 | | 55.1 | 45.3 | 52.5 | 48.8 | |
| M30 | | | | 0.0 | 131.6 | 113.5 | |
| M31 | | | | 0.0 | 126.6 | 149.1 | |
| M32 | 50.2 | 47.0 | 41.6 | 44.7 | 43.5 | 43.6 | |
| M33 | 55.4 | 47.6 | 65.3 | 60.1 | 47.6 | 70.3 | |
| M34 | 60.3 | 60.7 | | 65.2 | 55.2 | 64.1 | |
| M35 | 33.3 | 27.9 | 31.0 | 37.7 | 32.8 | 49.7 | |
| M36 | 38.8 | 29.5 | 24.3 | 40.8 | 28.8 | 17.5 | |
| M37 | 54.7 | 37.6 | | 29.8 | 56.8 | 24.6 | |
| M38 | 59.1 | 46.4 | 57.8 | 57.4 | | 43.6 | |

Tab. 2 - Standard skull measurements for specimens of Chinese species of *Sivalhippus* (mm).

**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.

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

C1-C52 refers to Characters 1-52 of Tab. 8.

**Institutional Abbreviations**

AMNH - American Museum of Natural History, New York

GSI - Geological Survey, Calcutta, India.

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

PMU - Paleontological Museum of Uppsala. M = vertebrate specimen. Currently named "The Museum of Evolution of Uppsala University".

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

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

## 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 *Sivalhippus* Lydekker, 1877

### ***Sivalhippus ptychodus*** (Sefve, 1927)

*Hipparion ptychodus* Sefve, 1927.
*Hipparion platyodus* Qiu et al., 1987 (in part).
"*Hipparion*" *ptychodus* Bernor et al., 1990.
"*Hipparion*" cf. *platyodus* Bernor et al., 1990.
"*Sivalhippus*" *ptychodus* Bernor and Lipscomb, 1991.

**Lectotype** (Bernor et al. 1990): PMUM347, an adult skull with right and left P2-M3, lacking the snout, anterior dentition and most of the cranium, housed in the Museum of Evolution of Uppsala University (Fig. 2).

**Type Locality**: Locality 73 (Andersson locality number; Fig. 1), Doujiaogou, Dongcun Village, Wuxiang County, Shanxi Province, China.

**Locality of new material**: In 1920, Licent initiated field work in Qingyang, Gansu and collected abundant vertebrate fossils from two localities, Xingjiagou and Zhaojiacha (Licent 1936). The mandible THP01839 described herein likely comes from one of these two localities.

**Stratigraphy and age**: 7- 6.5 Ma.

**Geographic Distribution** (Fig. 1): Yushe County, Shanxi Province; Shouyang County, Shanxi Province; Wuxiang County, Shanxi Province; Hequ County, Shanxi Province; Xinan County, Henan Province; Qingyang County, Gansu Province.

**Revised Diagnosis** (synapomorphies with *Sivalhippus* indicated in **bold ***):

Medium-size hipparion with cheek tooth row 134.8 - 142.2 mm. POB relatively long (44.7-50.2 mm in adult individuals); anteriormost limit of lacrimal placed well posterior to POF (**C1G***); nasolacrimal fossa absent (C2C); orbital surface of lacrimal bone with reduced foramen (C3B); POF placed anterodorsally on face, anteroposteriorly oriented (**C4K***), posterior pocketing slight (C5B), medially deep (C6A), medial wall morphology without internal pits (C7A), peripheral border moderately expressed (C8B), anterior rim faint (C9A); infraorbital foramen inferior to, or encroaching upon anteroventral border of the preorbital fossa (C10B); buccinator fossa distinctly limited (C11B) and not pocketed (C12A); caninus fossa absent (C13A); malar fossa absent (C14A); nasal notch approximately half the distance between canine and P2 (C15B) Maxillary and mandibular dP1 absent (C16C). Maxillary P2 anterostyle short (**C17A***); curvature of maxillary cheek teeth moderate (C18B); maximum cheek tooth height ca. 60 mm (C19C/D); cheek teeth with very complexly plicated fossettes (C20A,B), pre- and postfossette opposing borders separate (C21B), posterior wall of postfossette always distinct (C22B), pli caballins bifid or complex (C23A,B,C), hypoglyphs moderately to deeply incised (C24B,C), protocones short, lingually flattened and labially rounded (**predominately C25E*, also G and D; C26A***), protocone always isolated from protoloph (C27B) with no protocone spur (C28C), protocone more lingually placed than hypocone in premolars (C29B) and molars (C30B). Mandibular p2 with short and rounded anterostylid (C31B); Mandibular incisors are not grooved (C32A) and straight (C33B); i3 lateral aspect is elongate, not labiolingually constricted (C34A); premolar metaconid may be angular on the distal surface (**C35A,C***), molar metaconid angular on the distal surface (**C36A,C***), premolar metastylid angular on the mesial surface (**C37C***), premolar metastylid spur may be absent or present (C38A,B), molar metastylid angular on

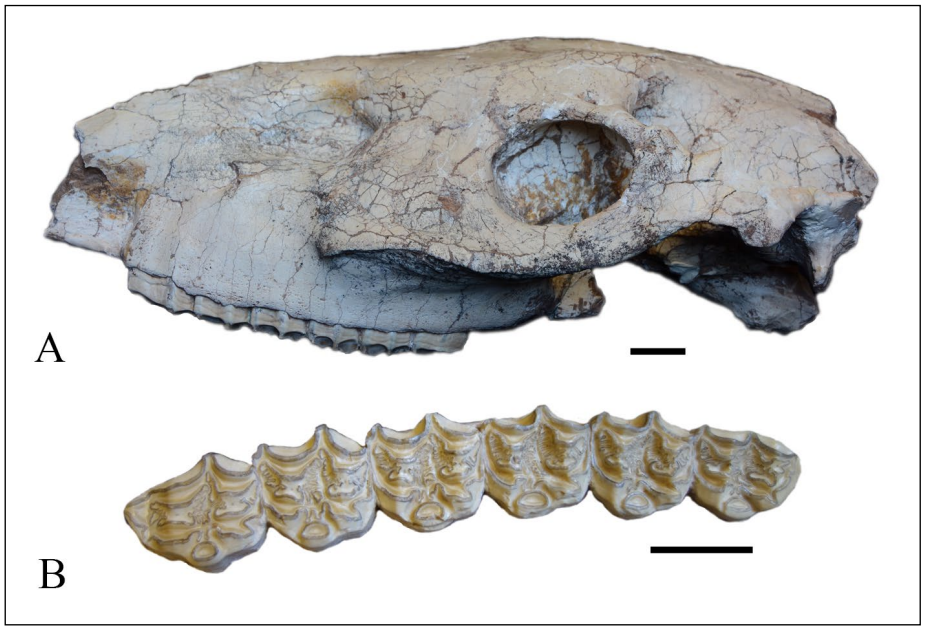


Fig. 2 - Skull of *S. ptychodus*, PMUM 347. A) left lateral view; B) occlusal view of left cheek tooth row. Scale bar = 2 cm.

the mesial surface (**C39C***), molars lacking metastylid spur (C40B), premolar ectoflexid may or may not separate metaconid and metastylid (C41A,B); molar ectoflexid separates metaconid and metastylid after early adult wear (C42 A,B); pli caballinid varies from being rudimentary or single to absent (C43B,C); protostylid varies from being placed on mesio-labial surface of the tooth to being a small pointed projection (C44B,F); protostylid orientation is vertically placed, lying lateral to protoconid band (C45C); ectostylids are absent (C46B); premolar linguaflexid varies from being shallow U-shaped to deep, broad U-shape (**C47C,D***); molar linguaflexid varies from being deep, broad U-shape to very broad and deep U-shape (**C48D,E***); preflexid morphology varies from having simple to complex margins (C49A,B,C); postflexid morphology varies from being simple to very complex (C50A,C); postflexid does not invade metaconid/metastylid junction by anteriormost portion bending sharply lingually (C51A); protoconid enamel band rounded (C52A).

**Description**

PMUM347 (Fig. 2A, B) is the Lectotype skull of *Sivalhippus ptychodus* (Bernor et al. 1990). The skull is medium size with P2-M3, 134.8 mm in length. The preorbital bar is very long, 50.2 mm with the anterior edge of the lacrimal placed less than ½ the distance from the anterior orbital rim to the posterior rim of the fossa; nasomaxillary fossa is absent; orbital surface of the lacrimal bone has a reduced foramen; POF is a small, rounded structure, POF ventral border distance to facial-maxillary crest, 38.8 mm; POF pocketing reduced with moderate to slight depth; fossa medial depth is deep, greater than 15 mm; preorbital fossa medial wall without internal pits; preorbital fossa peripheral border outline moderately delineated around the periphery; anterior rim is present; infraorbital foramen inferior to anteroventral border of POF; buccinator fossa not confluent with a caninus fossa; buccinator fossa not pocketed posteriorly; caninus fossa absent; malar fossa absent; nasal notch position cannot be determined. Maxillary dP1 is absent; P2 anterostyle is short; curvature of the cheek teeth is moderate; maximum cheek tooth crown height is estimated to be approximately 60 mm; maxillary cheek tooth fossette ornamentation is complex with several deeply amplified plications; pre- and postfossette opposing borders are not linked; posterior wall of postfossette is always distinct; pli caballin morphology is double to complex; hypoglyph is moderately deeply incised; protocone is lingually flattened and labially rounded on all cheek teeth; no protocone is connected to the protoloph; there are no protoconal spurs; premolar protocone more lingually placed than hypocone; molar protocone more lingually placed than hypocone.

PMUM3684 (Fig. 3 A, B) is an adult skull with a complete snout, lacking the posterior cranium. Muzzle length is 102.5 mm. P2-M3 is similar in length to PMUM347, 136.8 mm. POB length is slightly shorter than the Lectotype, 47.0 mm. POF

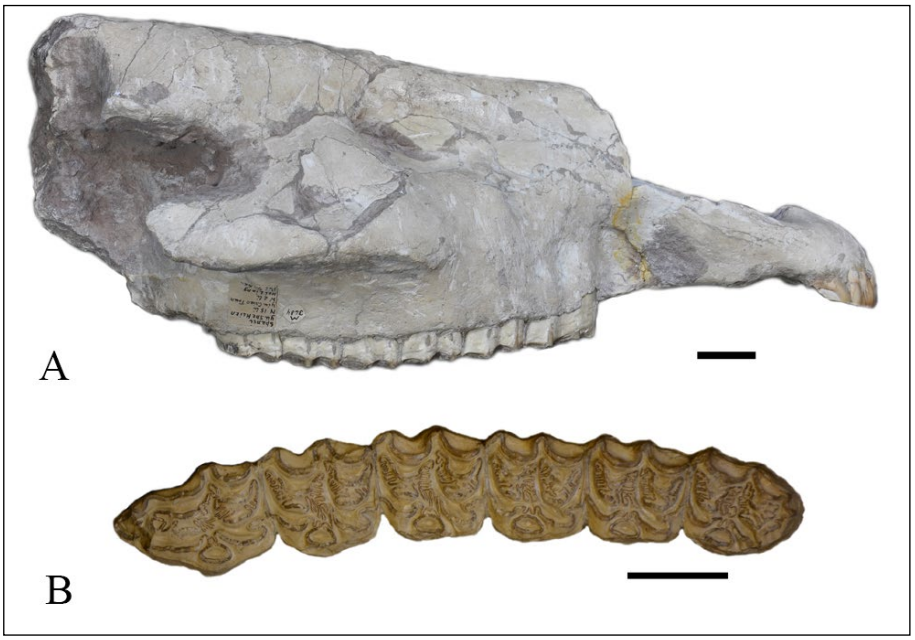


Fig. 3 - Skull of *S. ptychodus*, PMUM 3684. A) right lateral view; B) occlusal view of left cheek tooth row. Scale bar = 2 cm.

is shorter than in the Lectotype, 47.6 mm and has a dorsal-ventral height slightly less than the Lectotype, 27.9 mm. The distance from the ventral border of the POF to facial maxillary crest is less, 29.5 mm. As with the Lectotype, PMUM3684 has a POF that is placed high and far anteriorly on the face. The maxillary cheek teeth are lacking dP1, have a short anterostyle, cheek teeth are moderately curved, have an estimated maximum crown height of about 60 mm, fossette ornamentation is very complex; opposing borders of pre- and postfossette are separate; posterior wall of postfossette is always distinct; pli caballin is double to complex (on P3 and P4), hypoglyph is only moderately deeply incised; protocone shows some degree of lingual flattening, especially on P4-M3; protocone is moderately flattened, but less so than in the Lectotype; protocone is isolated from the protoloph on all cheek teeth; there are no protoconal spurs; premolar protocone is more lingually placed than the hypocone; molar protocone is more lingually placed than the hypocone.

PMUM350 is a juvenile skull fragment with P2-M2, lacking cranium, anterior nasals and snout (Bernor et al. 1990, fig. 12D from locality 114). POB length is shorter than the Lectotype, 41.6 mm; POF is longer than in the Lectotype, 65.3 mm; and has a dorsal-ventral height slightly less than the Lectotype, 31.0 mm. The distance from the ventral border of the POF to facial maxillary crest is much less, 24.3 mm. The cheek teeth reveal less plication complexity of the pre- and postfossettes, due to the very early stage of their wear. The pli caballins are single on P2 and M2, probably due to their early stage of wear, but bifid on P4-M1. Hypoglyphs are deeply incised. Protocones are lingually flattened on P4-M1, and elongate on the remaining cheek teeth, again probably due to the very early stage of wear (Bernor et al. 1990).

PMUM593 (re: Bernor et al. 1990, fig 12C) is an old adult individual with right P2-M3, left P3 (fragmentary)-M3, lacking posterior cranium, nasals and snout. Length of P2-M3 is 142.2 mm; POB length is shorter than the Lectotype, 44.7 mm; POF is longer than in the Lectotype, 60.1 mm; and has a dorsal-ventral height greater than the Lectotype, 37.7 mm. The distance from the ventral border of the POF to facial maxillary crest is greater than in the Lectotype, 40.8 mm. The cheek teeth are heavily worn due to the advanced age of the individual. This has resulted in increased rounding of the protocones, except on M3, which has retained a lingually flattened and labially rounded morphology, and simpler enamel plications.

AMNH143267 (= AMNH field number 91B979 of Bernor et al. 1990, tab. 4; Fig.4 A, B) is a well preserved skull with an associated mandible of an adult male individual. It is the most complete specimen of *Sivalhippus ptychodus*. Skull muzzle length is 108.8, significantly longer than M3684. P2-M3 length is very similar to the Lectotype, PMUM347, 133.8 mm. POB length is shorter than the Lectotype, 43.5 mm. POF is shorter than in the Lectotype, 47.6 mm and has a dorsal-ventral height

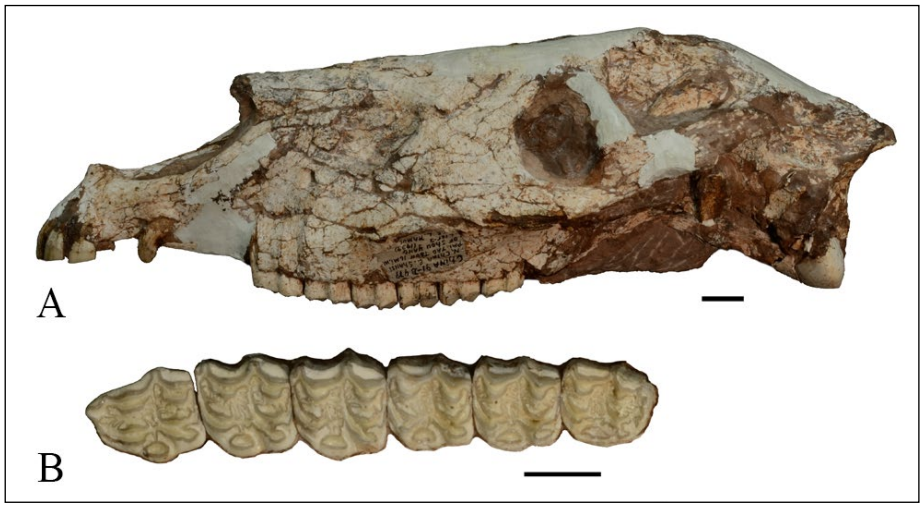


Fig. 4 - Skull of *S. ptychodus*, AMNH 143267. A) left lateral view; B) occlusal view of left cheek tooth row. Scale bar = 2 cm.

lesser than the Lectotype, 32.8 mm. The distance from the ventral border of the POF to facial maxillary crest is less, 28.8 mm, slightly less than M3684. The cranial features are identical to the Lectotype. The maxillary tooth characters are similar to those seen in the Lectotype, but the maxillary cheek tooth plications are less complex than those of the Lectotype (Fig. 4; Tab. 3).

Sefve (1927: text fig. 22, pg. 42) figured a right mandibular p2-m1 (occlusal view) of *Sivalhippus ptychodus* from Locality 73, Yushe Basin. An unfigured specimen PMUM353 is a left p2-m1 plus mesial portion of m2 that is likely the same individual as text fig. 22 (Fig. 7A herein). Characteristics of the specimen figured by Sefve (1927: text fig. 22, pg. 42) dentition include: premolar metaconid is angular on the distal surface of p3 and p4 and metastylid is angular on the mesial surface; p2-p4 ectoflexids are deep and closely approach the metaconid-metastylid isthmus; pli caballinid is rudimentary on p2-p4. The small- to medium length of the cheek tooth row is a character congruent with the maxillary dentitions of the *Sivalhippus ptychodus* hypodigm described above. Sefve (1927) also referred a right mandibular cheek tooth series, PMUM356 with p3-m3 to *S. ptychodus* with a similar morphology but having ectoflexid being shorter in p4, perhaps due to advanced wear (Fig. 7B). This is a later stage of wear dentition with rounded metaconids and angular metastylids, shallow premolar ectoflexids and very deep molar ectoflexids.

AMNH143267 (Fig. 5; 7D) is the best preserved mandible specimen of *Sivalhippus ptychodus*, with complete dentition including incisors and canines and the left cheek tooth row. Mandibular incisors are not grooved; they are straight; i3 lateral aspect is elongate, not labiolingually constricted. The p2 anterostylid is short and rounded. Premolar and molar metaconid are rounded; premolar and molar metastylid are angular on mesial surface; premolar-molar metastylid spurs are absent; premolar ectoflexid does not separate metaconid and metastylid whereas molar ectoflexid separates metaconid and metastylid; pli caballinid is rudimentary or single; protostylid is absent on occlusal surface, but may be on side of crown buried in cement; ectostylids are absent; premolar linguaflexid is shallow U-shaped; molar linguaflexid is deep, broad U-shape; preflexid and postflexid have simple margins; postflexid does not invade metaconid/metastylid junction by anteriormost portion bending sharply lingually; protoconid enamel band is rounded.

THP 01839 (Fig. 6; 7C; Tab. 4) is a mandibular fragment with left p2 to m3 and right p2 to m2 of a young adult with m3 in an early stage of occlusion. While the mandible is fragmentary, this specimen includes both right and left cheek tooth rows and has been preserved as early adult wear stage. The length of lower cheek tooth row is 146.0 mm which is slightly exaggerated by the slight separation of the teeth's interstitial spaces; the actual length would be somewhat less. As such, the size is close to the maxillary cheek tooth rows of the skulls described above. The p2 anterostylid is short and rounded; metaconid and metastylid are rounded; metastylid spur is present and strongly developed; ectoflexid is shallow and does not separate metaconid – metastylid; pli caballinid is strongly developed and single; protostylid and ectostylid are absent; linguaflexid is deep and U-shaped; preflexid and postflexid have

| ID | PMUM347 | | | | | | PMUM350 | | | | | PMUM593 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taxon | *S. ptychodus* Lectotype | | | | | | *S. ptychodus* | | | | | *S. ptychodus* | | | | | |
| Tooth | P2 | P3 | P4 | M1 | M2 | M3 | P2 | P3 | P4 | M1 | M2 | P2 | P3 | P4 | M1 | M2 | M3 |
| M1 | 28.2 | 23.1 | 22.8 | 20.4 | 19.4 | 21.1 | 31.5 | 25 | 23.5 | 23 | 22.6 | 13.5 | 21.6 | 23 | 20.7 | 21.8 | 23.5 |
| M2 | | | | | | | | | | | | | | | | | |
| M3 | 22.5 | 23.6 | 23 | 21.4 | 20.9 | 17.7 | 20.7 | 23.9 | 21.6 | 20.8 | 19.4 | 24.5 | 25.8 | 26.5 | 24.7 | 23.5 | 19.8 |
| M4 | | | | | | | | | | | | | | | | | |
| M5 | | | | | | | | | | | | | | | | | |
| M6 | | | | | | | | | | | | | | | | | |
| M7 | | | | | | | | | | | | | | | | | |
| M8 | | | | | | | | | | | | | | | | | |
| M9 | | | | | | | | | | | | | | | | | |
| M10 | 6.2 | 6.3 | 6.6 | 7 | 6 | 6.8 | 7.9 | 7.9 | 7.3 | 7.3 | 8.9 | | | 9.1 | 8.7 | 8.9 | 9.5 |
| M11 | 4.5 | 4.2 | 4.4 | 4.4 | 4.3 | 3.8 | 4.4 | 4.4 | 4.4 | 4.4 | 3.7 | | | 7.1 | 5.8 | 6 | 4.9 |

| ID | PMUM3684 | | | | | | | | | | AMNH143267 | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taxon | *S. ptychodus* | | | | | | | | | | *S. ptychodus* | | | | | | | | | |
| Tooth | I1 | I2 | I3 | C | P2 | P3 | P4 | M1 | M2 | M3 | I1 | I2 | I3 | C | P2 | P3 | P4 | M1 | M2 | M3 |
| M1 | 14.7 | 16.2 | 16.9 | 9.2 | 28.9 | 24.6 | 25.3 | 20.1 | 21.0 | 20.2 | 15.9 | 15.6 | 16.6 | 12.1 | 27 | 23 | 22.6 | 19.5 | 19.9 | 20.9 |
| M2 | | | | | | | | | | | | | | | | | | | | |
| M3 | 8.8 | 7 | 7.9 | 6.2 | 23.2 | 23.6 | 23 | 21.8 | 20.3 | 17.7 | 9.9 | 8.6 | 7.9 | 6.6 | 21.3 | 20.9 | 20.8 | 19.3 | 19.8 | 16.4 |
| M4 | | | | | | | | | | | | | | | | | | | | |
| M5 | | | | | 33 | | | | | | | | | | | | | | | |
| M6 | | | | | | | | | | | | | | | 2 | 3 | | 2 | 1 | 2 |
| M7 | | | | | | | | | | | | | | | 3 | 4 | 4 | 4 | 4 | 3 |
| M8 | | | | | | | | | | | | | | | 3 | 2 | 2 | 3 | 3 | 2 |
| M9 | | | | | | | | | | | | | | | 1 | 1 | 1 | 1 | 1 | 2 |
| M10 | | | | | 7.5 | 7.1 | 6.8 | 6.4 | 7.2 | 6.4 | | | | | 5.9 | 5.9 | 6.3 | 6.2 | 6.2 | 6.2 |
| M11 | | | | | 4.5 | 4.6 | 4.9 | 4.7 | 4.5 | 4.5 | | | | | 4 | 3.4 | 3.6 | 3.5 | 3.6 | 3.3 |

| ID | PMUM3691 | | | | | | | | | | THP22708 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taxon | *S. platyodus* lectotype | | | | | | | | | | *S. platyodus* | | | | | |
| Tooth | I1 | I2 | I3 | C | P2 | P3 | P4 | M1 | M2 | M3 | P2 | P3 | P4 | M1 | M2 | M3 |
| M1 | 15.4 | 16.2 | 15.6 | 12.9 | 33.1 | 26.1 | 25 | 20.9 | 21.4 | 23.4 | 32.2 | 24.2 | 22.4 | 22 | 21.5 | 19.1 |
| M2 | | | | | | | | | | | | | | | | |
| M3 | 9.2 | 7.1 | 6.5 | 7.3 | 25.1 | 26.6 | 26.3 | 23.5 | 22.7 | 19.7 | 20.1 | 21.6 | 21.1 | 20.6 | 19.5 | 15.5 |
| M4 | | | | | | | | | | | | | | | | |
| M5 | | | | | | | | | | | | | | | | |
| M6 | | | | | | | | | | | 4 | 2 | 3 | 4 | 5 | 3 |
| M7 | | | | | | | | | | | 7 | 7 | 7 | 9 | 8 | 5 |
| M8 | | | | | | | | | | | 2 | 3 | 4 | 7 | 6 | 2 |
| M9 | | | | | | | | | | | 1 | 1 | 1 | 3 | 2 | |
| M10 | | | | | 7 | 6.1 | 6.9 | 6.4 | 7.1 | 8.2 | 7.6 | 7.3 | 7.2 | 7.2 | 7 | 8.2 |
| M11 | | | | | 5 | 4.7 | 4.1 | 4.1 | 4.1 | 3.6 | 3.8 | 3.4 | 4 | 3.7 | 3.3 | 3.1 |

Tab. 3 - Standard maxillary cheek tooth measurements for specimens of Chinese species of *Sivalhippus* (mm).

complex margins; postflexid does not invade metaconid/metastylid junction by the rounded anteriormost portion bending sharply lingually; protoconid enamel band is rounded. The p3 metaconid is angular on the distal surface; metastylid is nearly triangular; pre- and postflexid are less complex than p2; other features are similar to p2 except that metaconid spur is weakly developed. The p4 is similar to p3 except for more complex pre- and postflexid margins, and flat protoconid enamel band; it is also the only tooth in the mandibular row with the postflexid invading metaconid/metastylid junction by rounded anteriormost portion bending sharply lingually. The m1 metaconid is subtriangular on the distal surface; metastylid is triangular on the mesial surface; metastylid spur is absent; ectoflexid is deep and separates metaconid and metastylid; preflexid has moderately complex margins; postflexid has simple margins; other features are similar to the premolar series. The m2 is similar to the m1 except for having a very complex preflexid margin. The m3 is of an early wear adult having a very shallow ectoflexid, complex postflexid margin, protoconid enamel band flattened.

THP 01839 has very strongly developed pli caballinids on p2-p4 while PMUM353 and AMNH143267 have rudimentary pli caballinids due to its more advanced age. PMUM353 also has pri-


Fig. 5 - Mandible of *S. ptychodus*, AMNH 143267. A) left lateral view; B) occlusal view. Scale bar = 2 cm.

mitive, deeply projecting ectoflexids on the premolars whereas THP 01839 has shallow ectoflexids on p2-p4 likely due to its young age. The hypodigm of skulls, maxillary and mandibular dentitions of *S. ptychodus* are very similar to each other in their size.

**Remarks**

Qiu et al. (1979) suggested that the geologic age of the Xingjiagou and Zhaojiacha faunas originated from the same stratigraphic horizon (Fig. 1). Deng (2006) correlated the Qingyang fauna, Gansu with European MN 12, ca.7 Ma, based on mammal biochronological correlations. The Lectotype of *Sivalhippus ptychodus,* PMUM347, was collected from the Wuxiang Basin, Shanxi. Another skull PMUM3684 originated from the Yushe Basin, Shanxi. Opdyke et al. (2013) correlated the base of the Mahui Fm., lowest formation of the Yushe Basin is ca. 6.5 Ma based on magnetostratigraphic data. Tedford et al. (2013) considered that the basal sediments of the Wuxiang Basin to be correlative with the Mahui Fm. because of similarities in their mammalian fauna, except for some subtle differences, such as the presence of *Eostyloceros blainvillei* (well known from older Baode Fm. faunas). Tedford et al. (2013) suggested that the age of the base of Wuxiang Basin is probably a little earlier than that of Yushe Basin. Therefore the age of PMUM347 and PMUM3684 is circa 7-6.5 Ma.

*Sivalhippus ptychodus* has very long preorbital bar, strong preorbital fossa placed dorsally high and far anteriorly (with long POB), shallow nasal notch, complex upper cheek teeth fossettes, lingually flattened and labially rounded protocones, deep hypoglyphs, double or complex pli caballins, triangular metaconid and metastylid and broad U-shaped linguaflexid. These features are strongly similar to *Sivalhippus perimensis* from the Siwaliks (Bernor & Hussain 1985; Bernor et al. 1990 and Wolf et al. 2013). *Sivalhippus platyodus* is similar to *S. ptychodus* differing in its larger POF dorsoventral dimension. We discuss this matter further below.

| ID | PMUM353 | AMNH 143268 | THP 01839 | PMUM3691 |
|---|---|---|---|---|
| Taxon | *S. ptychodus* | *S. ptychodus* | *S. ptychodus* | *S. platyodus* |
| M1 | | | | |
| M2 | 94.7 | 105.7 | | 93.7 |
| M3 | 69.3 | 69.1 | | 77.5 |
| M4 | | 63.2 | | 69 |
| M5 | | 132.5 | | 146 |
| M6 | | | | |
| M7 | 47.4 | 36.0 | | 46 |
| M8 | | | | |
| M9 | | | | |
| M10 | | 89.9 | | |
| M11 | | 66.1 | 58.8 | |
| M12 | 42.9 | 51.9 | 40.3 | 41.8 |
| M13 | 63.6 | 71.7 | | 79.5 |
| M14 | 31.5 | | | 29.8 |

Tab. 4 - Standard mandible measurements for specimens of Chinese species of *Sivalhippus* (mm).

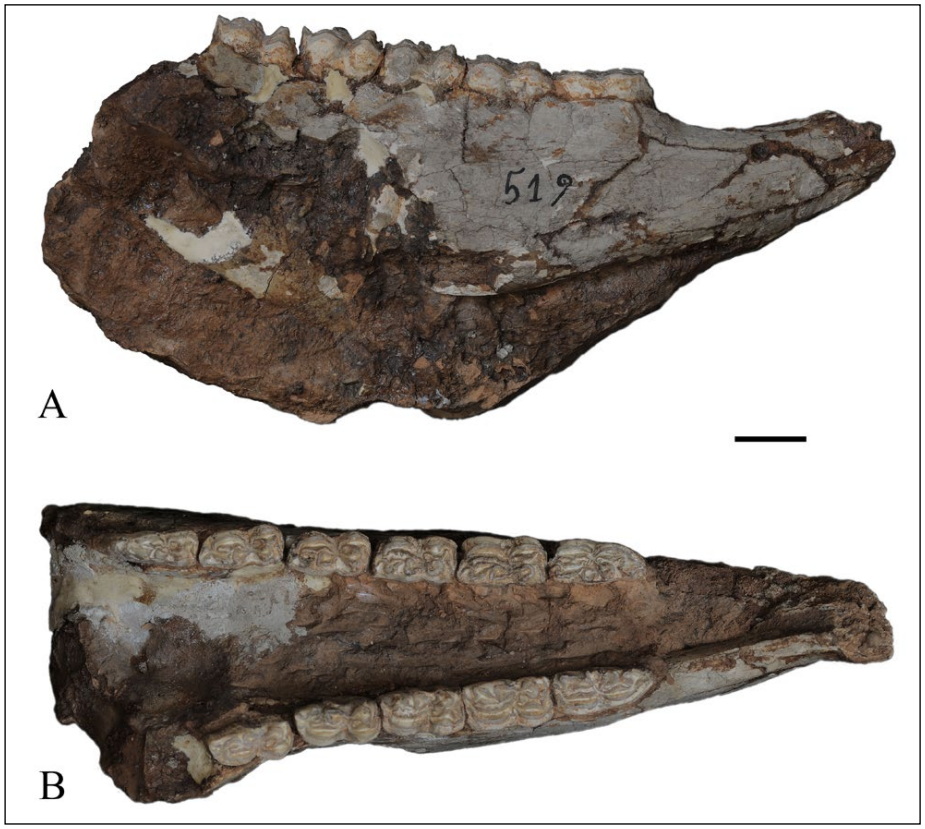


Fig. 6 - Mandible of *S. ptychodus*, THP 01839. A) right lateral view; B) occlusal view. Scale bar = 2 cm.

## ***Sivalhippus platyodus*** (Sefve, 1927)

*Hipparion platyodus* Sefve, 1927.
*Hipparion platyodus* Qiu et al., 1987 (in part).
"*Hipparion*" cf. *platyodus* Bernor et al., 1990.
"*Sivalhippus*" *platyodus* Bernor and Lipscomb, 1991.
*Hipparion platyodus* Deng et al., 2011.

**Lectotype** (Bernor et al. 1990): PMUM3691, an adult skull with right and left C-M3, housed in the Paleontological, Museum, University of Uppsala, Sweden (Fig. 8).

**Type Locality**: Locality 70 (Andersson locality number; Fig. 1), Wuxiang County, Shanxi Province, China

**Stratigraphy and age**: 7- 6.5 Ma.

**Geographic Distribution** (fig. 1): Yushe County, Shanxi Province; Wuxiang County, Shanxi Province.

**Revised Diagnosis** (synapomorphies with *Sivalhippus* indicated in **bold ***):

Medium-size hipparion with cheek tooth row 140.0-149.0 mm. POB relatively long (43.6 mm in the Lectotype PMUM3691); anteriormost limit of lacrimal placed well posterior to POF (C1C**,** primitive as in *S. nagriensis*); nasomaxillary fossa absent (C2C); orbital surface of lacrimal bone with reduced foramen (C3B); POF subtriangular shape and anteroventrally oriented (C4D), posterior pocketing slight (C5B), moderately deep (C6B), medial wall morphology without internal pits (C7A), peripheral border moderately expressed (C8B), anterior rim faint (C9A); infraorbital foramen inferior to, or encroaching upon anteroventral border of the preorbital fossa (C10B); buccinator fossa distinctly limited (C11B) and not pocketed (C12A); caninus fossa absent (C13A); malar fossa absent (C14A); nasal notch at or near the anterior border of P2 (C15C) Maxillary and mandibular dP1 absent (C16C). Maxillary P2 anterostyle elongated (C17B); curvature of maxillary cheek teeth moderate (C18B); maximum cheek tooth height nearly 60 mm (C19C); cheek teeth with complexly plicated fossettes (C20A), pre- and postfossette opposing borders separate (C21B), posterior wall of postfossette always distinct (C22B), pli caballins mostly bifid or complex (C23A,C), hypoglyphs deeply incised (C24B), protocones short, lingually flattened and labially rounded (**predominately C25E*, also G and D; C26A***), protocone always isolated from protoloph (C27B) with no protocone spur (C28C), protocone more lingually placed than hypocone in premolars (C29B) and molars (C30B). Mandibular p2 with modestly elongate anterostylid in the Lectotype PMUM3691 (C31A); Mandibular incisors are not grooved (C32A) and straight (C33B); i3 lateral aspect is elongate, not


Fig. 7 - Occlusal view of cheek tooth row of *S. ptychodus*. A) PMUM353, left side; B) PMUM353, right side; C) THP 01839, left side; D) AMNH 143267, left side. Scale bar = 2 cm.

labiolingually constricted (C34A); premolar metaconid is rounded on the distal surface (C35A), molar metaconid angular on the distal surface (C36C), premolar metastylid angular on the mesial surface (**C37C***), premolar metastylid spur is absent (C38B), molar metastylid angular on the mesial surface (**C39C***), molars lacking metastylid spur (C40B), premolar ectoflexid does not separate metaconid and metastylid (C41A); molar ectoflexid separates metaconid and metastylid (C42B); pli caballinid varies from being rudimentrary or single (C43B); protostylid present on occlusal surface as an enclosed enamel ring (C44A); protostylid orientation unknown (C45); ectostylids are absent (C46B); premolar linguaflexid shallow U-shape (**C47C***); molar linguaflexid is a very deep broad U-shape(**C48E***); preflexids have complex margins (C49B); postflexids have complex margins (C50B); postflexid does not invade metaconid/metastylid junction by anteriormost portion bending sharply lingually (C51A); protoconid enamel band is rounded (C52A).

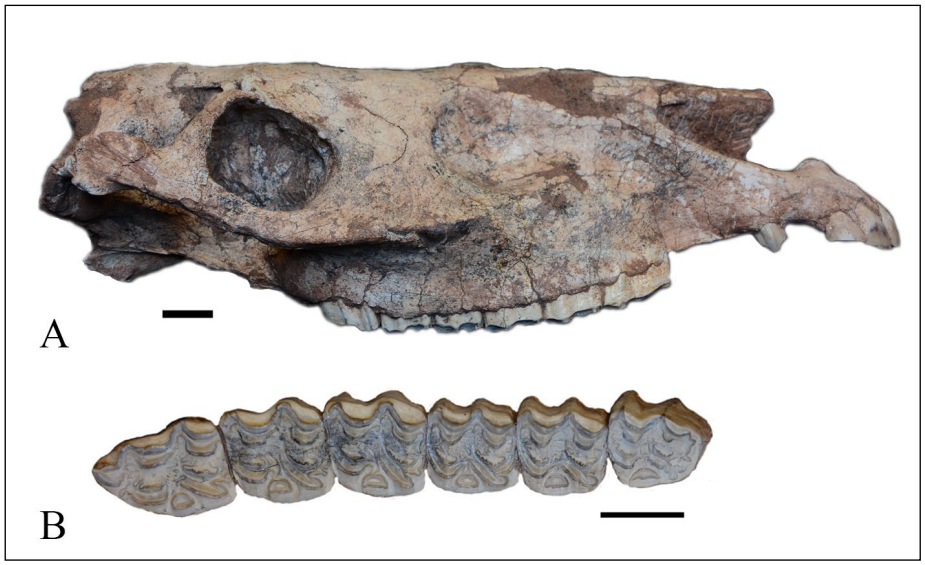


Fig. 8 - Skull of *S. platyodus*, PMUM 3691. A) right lateral view; B) occlusal view of left cheek tooth row. Scale bar = 2 cm.

| ID | AMNH 143269 | | | | | | | | | | PMUM3691 | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taxon | *S. ptychodus* | | | | | | | | | | *S. platyodus* lectotype | | | | | | | | | |
| Tooth | i1 | i2 | i3 | c | p2 | p3 | p4 | m1 | m2 | m3 | i1 | i2 | i3 | c | p2 | p3 | p4 | m1 | m2 | m3 |
| M1 | 13.5 | 14.5 | 13.5 | 10.2 | 24.8 | 21.2 | 21.1 | 20.5 | 19.8 | 22.2 | 12.5 | 14.1 | 14.1 | 11.0 | 28.7 | 24.5 | 23.8 | 22 | 22.1 | 24.6 |
| M2 | | | | | | | | | | | | | | | | | | | | |
| M3 | 9.9 | 8.8 | 7.6 | 7.6 | 9.9 | 12.3 | 11.7 | 11.5 | 11.3 | 9.4 | 9.6 | 9.6 | 8.3 | 8.3 | 11.9 | 15.3 | 14.7 | 13.8 | 12.6 | 10.7 |
| M4 | | | | | 7.8 | 7.5 | 11.3 | 5.7 | 5.5 | 5.6 | | | | | 8.4 | 6.3 | 6.1 | 6.2 | 6.3 | 6.1 |
| M5 | | | | | 11.3 | 11.6 | 10.2 | 8.4 | 8.4 | 7.1 | | | | | 12.6 | 12.8 | 12 | 8.4 | 8.7 | 8.4 |
| M6 | | | | | 12.9 | 13.9 | 13.5 | 11.7 | 11 | 9.7 | | | | | 13.2 | 16.8 | 17.3 | 12.7 | 12.1 | 12 |
| M7 | | | | | | | | | | | | | | | | | | | | |
| M8 | | | | | 9.9 | 11 | 11 | 9.9 | 9.5 | 7.5 | | | | | 10.1 | 13.3 | 13.1 | 11.1 | 11.2 | 10.1 |
| M9 | | | | | 11.5 | 11.4 | 10.8 | 9.1 | 8 | 6.7 | | | | | 11.8 | 13.4 | 12.2 | 10.2 | 9.8 | 8.5 |

| ID | THP 01839 | | | | | | PMUM353 | | | | | | | | PMUM356 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taxon | *S. ptychodus* | | | | | | *S. ptychodus* | | | | | | | | *S. ptychodus* | | | | | |
| Tooth | p2 | p3 | p4 | m1 | m2 | m3 | i1 | i2 | i3 | c | p2 | p3 | p4 | m1 | p3 | p4 | m1 | m2 | m3 | |
| M1 | 26.0 | 23.7 | 23.1 | 22.8 | 23.9 | 22.5 | 10.3 | 12.2 | 12.3 | 9.4 | 26.1 | 22.4 | 21.7 | 19.0 | 23.4 | 23.8 | 21.6 | 22.1 | | |
| M2 | | | | | | | | | | | | | | | | | | | | |
| M3 | 9.6 | 12.2 | 10.8 | 12.5 | 11.4 | 9.2 | 9.6 | 9.7 | 7.9 | 7.4 | 9.9 | 13.2 | 12.1 | 11.6 | 13.4 | 14.3 | 12.4 | 12.9 | 11 | |
| M4 | 8.1 | 8.3 | 7.1 | 7.7 | 7 | 6.8 | | | | | 6 | 7.8 | 7.9 | 5.8 | 7.5 | 8.1 | 5.8 | 6.6 | 6.4 | |
| M5 | 11.6 | 11.8 | 10.8 | 9.5 | 9.2 | 6.6 | | | | | 12 | 11.5 | 11.3 | 6.4 | 11 | 11.3 | 7.1 | 7.9 | 9.5 | |
| M6 | 11.8 | 13.6 | 12 | 10.1 | 9.4 | 8.6 | | | | | 12 | 13.8 | 13.3 | 11.4 | 15.9 | 16 | 13.9 | 14.4 | 13.6 | |
| M7 | | | | | | | | | | | | | | | | | | | | |
| M8 | 9.4 | 10.9 | 10.2 | 9.5 | 9.1 | 7.9 | | | | | 9.5 | 11.7 | 12.1 | 10.5 | 13.7 | 13.4 | 12.3 | 11 | 10 | |
| M9 | 10.5 | 11.2 | 9.5 | 9.3 | 9.2 | 7.1 | | | | | 11.3 | 11.4 | 10.8 | 10.1 | 13 | 12.3 | 10.6 | 10.1 | 9 | |

Tab. 5 - Standard mandibular teeth for specimens of Chinese species of *Sivalhippus* (mm).

| ID | NHMW A4229 | FAM 71800 | AMNH 19761 | PMUM 3691 | THP 22708 | PMUM 347 | PMUM 3684 | PMUM 350 | PMUM 593 | AMNH 143267 |
|---|---|---|---|---|---|---|---|---|---|---|
| Taxon | *H. primigenium* | *C. occidentale* | *S. perimensis* | *S.platyodus* | | | | *S.ptychodus* | | |
| Country | Austria | USA | IndoPakistan | China | China | China | China | China | China | China |
| AGE(Ma) | 10.5 | 10.5 | 8.0 | 7.0 | 7.0 | 7.0 | 7.0 | 7.0 | 7.0 | 7.0 |
| M1 | 136.6 | 110.7 | 116.8 | 98.8 | 97.0 | | 102.5 | | | 108.8 |
| M9 | 160.0 | 140.3 | 153.0 | 149.2 | 140.0 | 134.8 | 136.8 | | 142.2 | 133.8 |
| M32 | 47.2 | 39.7 | 56.2 | 43.6 | | 50.2 | 47.0 | 41.6 | 44.7 | 43.5 |
| M33 | 76.8 | 71.3 | 49.2 | 70.3 | 64.9 | 55.4 | 47.6 | 65.3 | 60.1 | 47.6 |
| M35 | 56.2 | 39.3 | 29.1 | 49.7 | 44.9 | 33.3 | 27.9 | 31.0 | 37.7 | 32.8 |
| M36 | 32.7 | 32.0 | 35.0 | 17.5 | 29.7 | 38.8 | 29.5 | 24.3 | 40.8 | 28.8 |

Tab. 6 - Measurements of key characters of skull for *Cormohipparion occidentale* (FAM: 71800), *Sivalhippus perimensis* (AMNH19761) and Chinese species of *Sivalhippus* (mm), *Hippotherium primigenium* (Vienna Basin Pannonian C-D, NHMWA4229) standard.

## Description

PMUM3691 (Fig. 8) is the Lectotype skull of *Sivalhippus platyodus* (Bernor et al. 1990). The skull is of an adult male, medium size with snout being 98.8 mm in length. The P2-M3 length is 149.2 mm. The nasomaxillary fossa is absent; orbital surface of the lacrimal bone has a reduced foramen; POB is 43.6 mm in length. POF is 70.3 mm in length with a dorso-ventral height of 49.7 mm, subtriangular shaped and anteroventrally oriented; POF ventral border

Fig. 9 - Occlusal view of mandible of *S. platyodus*, PMUM3691. Scale bar = 2 cm.

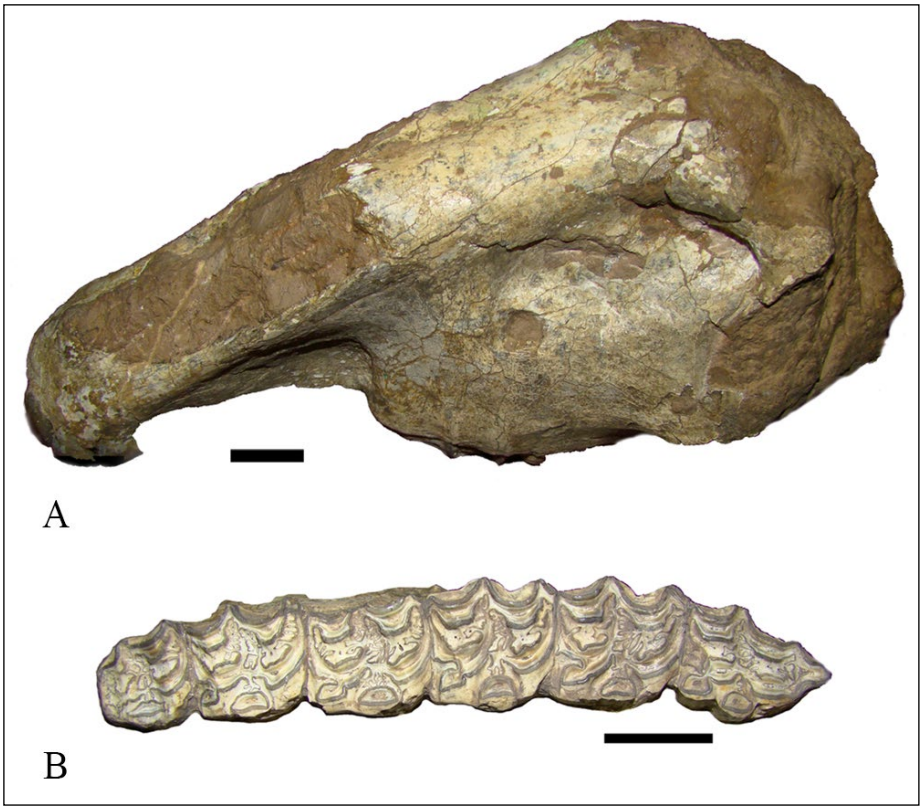


Fig. 10 - Skull of *S. platyodus*, THP 22708. A) left oblique view; B) occlusal view of right cheek tooth row. Scale bar = 2 cm.

distance to facial-maxillary crest is 17.5 mm; POF pocketing reduced with moderate to slight depth; fossa medial depth is deep, greater than 15 mm; preorbital fossa medial wall without internal pits; preorbital fossa peripheral border outline is moderately well delineated around the periphery; anterior rim is present; infraorbital foramen inferior to anteroventral border of POF; buccinator fossa not confluent with a caninus fossa; buccinator fossa is not pocketed posteriorly; caninus fossa absent; malar fossa absent; nasal notch position cannot be determined. Maxillary dP1 is absent; P2 anterostyle is moderately elongated; curvature of the cheek teeth is moderate; maximum cheek tooth crown height is estimated to be approximately 40-60 mm; maxillary cheek tooth fossette ornamentation is complex with several deeply amplified plications; pre- and postfossette opposing borders are not linked; posterior wall of postfossette is always distinct; pli caballin morphology varies from double/complex to single (on M2 and M3); hypoglyph is deeply incised; protocone is lingually flattened and labially rounded; no protocone is connected to the protoloph; there are no protoconal spurs; premolar protocone more lingually placed than hypocone; molar protocone more lingually placed than hypocone.

PMUM3691 (Fig. 9) mandibular incisors are not grooved; they are straight; i3 lateral aspect is elongate, not labiolingually constricted. The p2 anterostylid is elongated. Premolar and molar metaconids are rounded; premolar and molar metastylid are angular on mesial surface except for the right M3; premolar-molar metastylid spurs are absent; premolar ectoflexid closely approaches but does not separate metaconid and metastylid whereas molar ectoflexid separates metaconid and metastylid; pli caballinid is rudimentary or lacking; protostylid is present on occlusal surface often as an enclosed enamel ring; ectostylids are absent; premolar linguaflexid is shallow U-shape; molar linguaflexid is a deep U-shape; preflexid and postflexids have complex margins; postflexid does not invade metaconid/metastylid junction by anteriormost portion bending sharply lingually; protoconid enamel band is rounded.

THP22708 (Fig. 10) is a medium-sized adult female skull with a complete snout, lacking the posterior cranium. Compared to the Lectotype of *Sivalhippus platyodus*, muzzle length virtually the same, 97.0 mm; P2-M3 is shorter, 140.0 mm.; POF is shorter, 64.9 mm and has a dorsal-ventral height shorter than the Lectotype, 44.9 mm; distance from the ventral border of the POF to facial maxillary crest is greater, 29.7 mm. As with the Lectotype,


Fig. 11 - Left metacarpal III of *S. platyodus*, IVPP V 8247. A) cranial view; B) caudal view; C) proximal view; D) distal view. Scale bar = 2 cm.

PMUM3684 has a POF that is placed high and far anteriorly on the face. The other cranial and dental features are as in the Lectotype.

IVPPV8247 is a left MCIII found from Changyin locality, Yushe Basin (Fig. 11). It is very short and robust (Tab. 7), resembles those of typical *Sivalhippus* (Wolf et al. 2013). Articular facets with MCII and MCIV are large, which show that it has very robust medial and lateral metacarpals.

**Remarks**

*Sivalhippus platyodus* is morphologically similar to *Sivalhippus ptychodus* (Bernor et al. 1990; Wolf et al. 2013). These two species also overlap in their geographic distribution (Fig. 1). The long preorbital bar, large and subtriangular preorbital fossa, shallow nasal notch, complex upper cheek tooth fossettes, protocones that are lingually flattened and labially rounded, metaconid-metastylid with angular facing border and broad U-shaped linguaflexid of this species support its referral to the genus *Sivalhippus* (Fig. 5). Zhegallo (1978) regarded *S. platyodus* as a subspecies of *S. theobaldi*. Wolf et al. (2013) demonstrated that *Sivalhippus theobaldi* is much larger with very

| M1 | M2 | M3 | M4 | M5 | M6 | M7 |
|---|---|---|---|---|---|---|
| 171.3 | 165.4 | 27.0 | 19.4 | 36.3 | 24.2 | 31.9 |
| **M8** | **M9** | **M10** | **M11** | **M12** | **M13** | **M14** |
| 9.8 | 5.6 | 37.8 | 34.9 | 24.0 | 20.4 | 23.7 |

Tab. 7 - Measurements of left MCIII of *Sivalhippus platyodus*, V8247 (mm).

robust metapodials but referred *S. platyodus* to the genus *Sivalhippus* because of a number of synapomorphies: shallow nasal notch, strong subtriangular preorbital fossa, long preorbital bar, complex folds of upper cheek teeth, lingually flattened and labially rounded protocones and triangular double knots of lower cheek teeth.

According to known *S. platyodus* material described by Qiu et al. (1987) and Bernor et al. (1990), this species has many similarities as Siwaliks hipparion horses listed above. The highly robust metapodial is another diagnostic character of *S. platyodus*. Qiu et al. (1987) reported a very short and robust MC III from Yushe Basin (Fig.11). As listed by Wolf et al. (2013), the metapodial specimens of *Sivalhippus perimense, S. theobaldi* and *S. anwari* are all robust. Qiu et al. (1987) regarded *Sivalhippus ptychodus* as a synonym of *S. platyodus*. Later Bernor et al. (1990) reiterated the validity of *S. ptychodus*, stating that this species is unique compared to other Chinese hipparionines in its placement of the facial fossa far anteriorly and high dorsally above the plane of the facial-maxillary crest.

With our observations herein, the differences between *S. ptychodus* and *S. platyodus* are observed on the cranium. The Lectotype *Sivalhippus platyodus* PMUM3691 (Bernor et al. 1990 Fig. 4A&B) has a shorter POB, longer and deeper POF positioned closer to the facial-maxillary crest. The POF is larger and not positioned high on the face. The maxillary cheek teeth of *S. platyodus* have persistently labially rounded and lingually flattened protocones as in Siwalik *Sivalhippus perimensis* (Wolf et al. 2013) and like *S. ptychodus*. The Lectotype mandible of *Sivalhippus platyodus* (PMUM3691; Bernor et al. 1990, fig 4C) has rounded premolar and molar metaconids while having angular premolar and molar metastylids; whereas most specimens of *S. ptychodus* have more angular metaconid and metastylid. However, the mandible AMNH143267 has rounded metaconids both on premolar and molar (Fig. 7D). This makes it difficult to distinguish *S. ptychodus* and *S. platyodus*

based on mandibular cheek teeth alone. The mandibular cheek teeth of *Sivalhippus ptychodus* also have p2s with shorter anterostylids that are seen on all of our specimens: it is a stable feature. Whereas the Lectotype of *S. platyodus*, M3691 has elongated anteorstylid on p2 it is shorter on specimens of *S. ptychodus*. The specimens of *Sivalhippus perimensis*, AMNH19466 and AMNH19761 crania are larger than both *S. ptychodus* and *S. platyodus* (Wolf et al. 2013). Chinese species of *Plesiohipparion* and *Proboscidipparion* and African *Eurygnathohippus* evolve even more extreme angular metaconids and metastylids on the cheek teeth (Bernor & Sun 2015).

## Discussion

*Sivalhippus ptychodus* shares with *Sivalhippus perimensis* a POF that is placed dorso-ventrally high and far anterior on the face. Other lineages of hipparionine horses have long preorbital bars and large, dorsoventrally extensive POF such as is found in *S. platyodus*: *Cormohipparion* spp. and *Hippotherium* spp (Bernor et al. 1997, 2011; Bernor & White 2009). Most species of *Cormohipparion* group are distributed in North America. *Cormohipparion* was the lineage that populated Eurasia and Africa and is known from Sinap, Turkey, (Bernor et al. 2003), Bou Hanifia, Algeria (Bernor & White 2009) and Ethiopia (Bernor et al. 2010; 2017). *Hippotherium* was a successful clade that ranged from Central Europe eastward to the Balkans and Turkey including the following taxa: *Hippotherium* sp. (Vienna Basin, Pannonian C; Bernor et al. 2017), *Hippotherium primigenium* (Central Europe, Bernor et al. 1988; 1997), *Hippotherium brachypus* (Greece and Iran, Koufos 1987; Bernor et al. 2016), *Hippotherium intrans* (Hungary, Kretzoi 1983; Bernor et al. 2004); *Hippotherium microdon* (Hungary, Kormos 1914), *Hippotherium kammerschmitti* (Germany, Kaiser et al. 2003) and *Hippotherium malpassi* (Italy, Bernor et al. 2011). Chinese hipparion species similar to *Hippotherium* include "*Hippotherium*" *weihoense* and "*Hippotherium*" *chiai* (Qiu et al. 1987).

Bernor and White (2009) analyzed key measurements for distinguishing clades of Old World Hipparions: M1 = snout length; M9 = cheek tooth row length; M32 = POB length; M33 = POF length; M35 = POF dorsoventral height; M36 = distance from ventral border of POF to facial-maxillary crest. Table 6 provides the key measurements that we use to compare North American *Cormohipparion occidentale* (FAM 71800), Siwalik *Sivalhippus perimensis* (AMNH19761) and China *Sivalhippus ptychodus* and *Sivalhippus platyodus* specimens discussed herein. We use the *Hippotherium primigenium* from Inzersdorf (NHMWA4229) as our standard and plot the log10

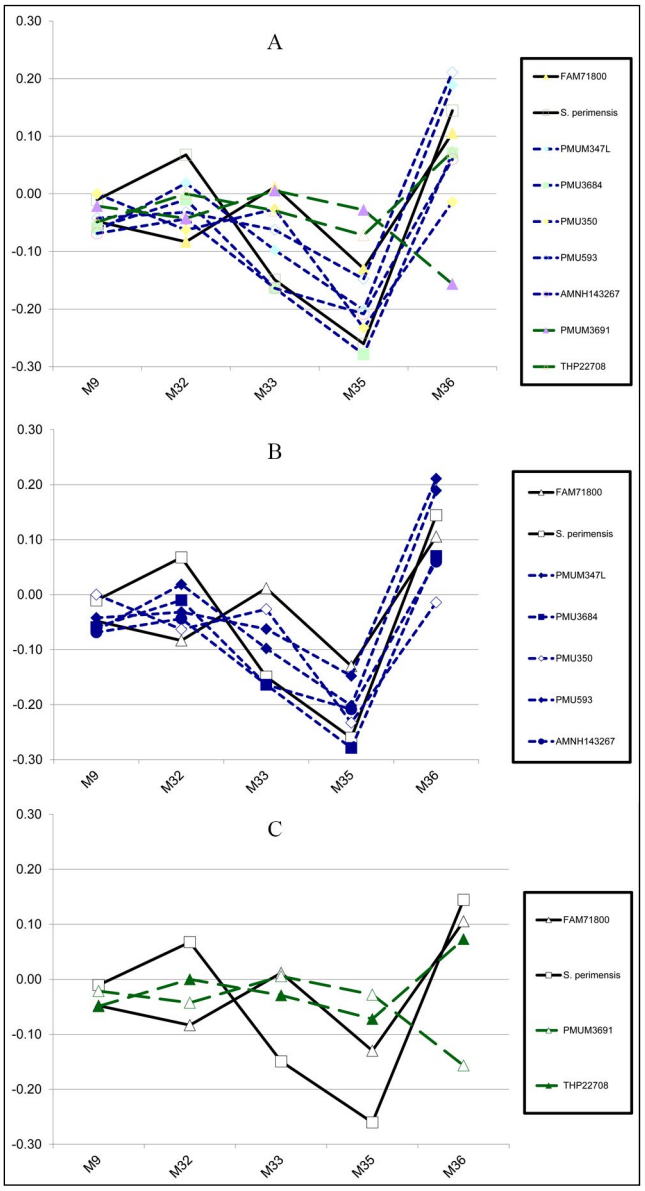


Fig. 12 - Ratio diagrams of skull measurements of *Sivalhippus* and other hipparion horses. Log10 Standard is Inzersdorf hipparion, *Hippotherium primigenium* (zero line).
A) Critical measurements on FAM71800 *Cormohipparion occidentale*, *Sivalhippus perimensis* and Chinese *Sivalhippus,* Log10 Ratios. B) Critical skull measurements on FAM71800 *Cormohipparion occidentale, Sivalhippus perimensis* and *Sivalhippus ptychodus*. C) Critical skull measurements in *Cormohipparion occidentale, Sivalhippus perimense* and *Sivalhippus platyodus*. Measurement numbers: M9, upper cheek teeth length; M32, distance between the orbit and the preorbital fossa; M33, length of the preorbital fossa; M35, height of the preorbital fossa; M36, distance between the preorbital fossa and the facial crest.

| Taxa | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PMUM347 | G | C | B | K | B | A | A | B | A | B | B | A | A | A | | C | A | B |
| PMUM3684 | G | C | B | K | B | A | A | B | A | B | B | A | A | A | B | C | A | B |
| PMUM350 | G | C | B | K | B | A | A | B | A | B | B | A | A | A | | | | |
| PMUM593 | G | C | B | K | B | A | A | B | A | B | B | A | A | A | | | | |
| PMUM353 | | | | | | | | | | | | | | | | | | |
| PMUM356 | | | | | | | | | | | | | | | | | | |
| THP01839 | | | | | | | | | | | | | | | | | | |
| AMNH143267 | G | C | B | K | B | A | A | B | A | B | B | A | A | A | C | C | A | B |
| PMUM3691 | C | C | B | D | B | B | A | B | A | B | B | A | A | A | C | C | B | B |
| THP22708 | | C | B | D | B | B | A | B | A | B | B | A | A | A | C | C | B | B |

| Taxa | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PMUM347 | C/D | A | B | B | A,C | C | E | A | B | C | B | B | | | | | | |
| PMUM3684 | C/D | A | B | B | A,C | C | E | A | B | C | B | B | | | | | | |
| PMUM350 | | B | | | A,B | B | D,E | | | | | | | | | | | |
| PMUM593 | | B | | | | | G,E | | | | | | | | | | | |
| PMUM353 | | | | | | | | | | | | | B | | | | C | |
| PMUM356 | | | | | | | | | | | | | | | | | C | C |
| THP01839 | | | | | | | | | | | | | B | | | | C | C |
| AMNH143267 | | A | B | B | A,B | B | E | A | B | C | B | B | B | A | B | A | A | A |
| PMUM3691 | C | A | B | B | A,C | B | E | A | B | C | B | B | A | A | B | A | A | A |
| THP22708 | C | A | B | B | A,C | B | E | A | B | C | B | B | | | | | | |

| Taxa | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PMUM347 | | | | | | | | | | | | | | | | |
| PMUM3684 | | | | | | | | | | | | | | | | |
| PMUM350 | | | | | | | | | | | | | | | | |
| PMUM593 | | | | | | | | | | | | | | | | |
| PMUM353 | C | B | C | B | B | | C | B | | B | D | | A | A | A | A |
| PMUM356 | C | B | C | B | A | B | C | F | C | B | D | E | A | A | A | A |
| THP01839 | C | A | C | B | A | A | B | B | | B | C | D | B,C | C | A | A |
| AMNH143267 | C | B | C | B | A | B | B | B | | B | C | D | A | A | A | A |
| PMUM3691 | C | B | C | B | A | B | B | A | | B | C | E | B | B | A | A |
| THP22708 | | | | | | | | | | | | | | | | |

Tab. 8 - Summary character state distributions of *Sivalhippus ptychodus* and *Sivalhippus platyodus* skulls, maxillary and mandibular dentitions.

ratios for the comparative samples (Fig. 12 A-C).

Fig. 12 plots skulls of Chinese specimens of *Sivalhippus ptychodus* and *Sivalhippus platyodus* compared to North American *C. occidentale* (FAM: 71800 following Bernor et al. 2003; Bernor & White 2009), Siwalik *S. perimensis* (AMNH19761) with Pannonian D-E *H. primigenium* from Inzersdorf (NHMWA4229) being the log10 standard. Fig. 12A plots all Chinese *Sivalhippus* together with North American *C. occidentale* and Siwalik *S. perimensis*. Fig. 12B plots *C. occidentale* and *S. perimensis* compared to Chinese *Sivalhippus ptychodus* only and Fig. 12C plots *C. occidentale* and *S. perimensis* compared to *Sivalhippus platyodus* only. A number of clear morphological distinctions can be made between the taxa under consideration (Tab. 6 and Fig. 12A-C). The *H. primigenium* standard from Inzersdorf, Austria is the largest taxon with the longest cheek tooth row (M9), *S. perimensis* has a slightly shorter tooth row and all Chinese *Sivalhippus* have shorter cheek tooth rows than both. Siwalik *S. perimensis* is the most derived taxon in the length of the POB (M32 = 56.2mm) and restriction of the POF high on the face (M35 = 29.1, M36 = 35.0 mm). Figures 12B and 12C exhibit clear distinctions between *Sivalhippus ptychodus* (Fig. 12B) and *S. platyodus* (Fig. 12C): *S. ptychodus* has all measurements for POF height (M35) falling below North American *C. occidentale* as is found for Siwalik *S. perimensis*; *S. platyodus* has all measurements for POF height falling above that for *C. occidentale*. Lectotype of *Sivalhippus ptychodus* (PMUM347) is of only moderate size (M9 = 134.8 mm) but has a very long POB (M32 = 50.2 mm) comparing closely with *S. perimensis*, albeit being smaller.

Bernor et al. (1988; 1996) and Woodburne (2007) argued that *Cormohipparion* was the ancestral group from which Old World hipparion evolved. *Cormohipparion occidentale* was believed to be the ancestral type for Old World hipparionine horses (Bernor et al. 2003). *Cormohipparion sinapensis* (Sinap,

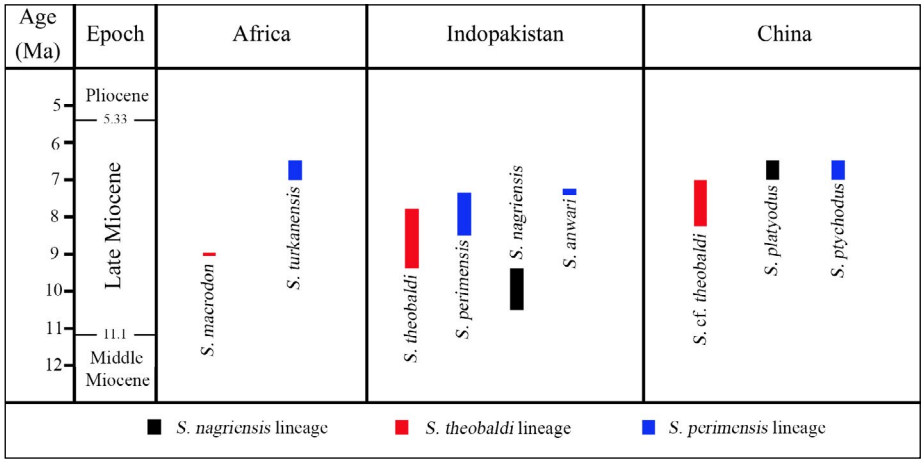


Fig. 13 - Geological distribution of *Sivalhippus* lineages in Indopakistan, China and Africa showing their phylogenetic relation and dispersal events. *Sivalhippus nagriensis* lineage (*S. nagriensis* and *S. platyodus*) in black; *Sivalhippus theobaldi* lineage in red (*S. theobaldi* , *S. macrodon,* and *S.* cf. *theobaldi*); *Sivalhippus perimensis* lineage (*S. perimensis, S. turkanensis*, *S. anwari* and *S. ptychodus*) in blue.

Turkey 10.8 Ma) and *Hippotherium primigenium* (Central Europe, ca. 11.4-11.0 Ma.) are the two oldest and most primitive Old World hipparion lineages; *C. occidentale* occurred in Indopakistan, Turkey and Africa while *H. primigenium* evolved originally in Central Europe (Bernor et al. 2017). In these lineages the POF is characterized as being large, dorsoventrally and anteroposteriorly extensive, medially deep and posteriorly pocketed with accompanying long POB. Species of these primitive lineages also have a POF positioned closer to the facial-maxillary crest. Morphometric analysis by Bernor et al. (2003) and phylogenetic analysis of Woodburne (2007) showed that North American early late Miocene *C. matthewi* and *C. occidentale* were sister taxa and formed the most derived clade within the American *Cormohipparion*. Woodburne (2009) considered that another *Cormohipparion, Cormohipparion* sp. from the Punchbowl Formation, California, was the likely source of the Old World "*Hipparion*" Datum and radiation. This was supported by Bernor et al.'s (2017) analysis of Vienna Basin Pannonian C hipparions.

The Siwaliks, Indopakistan, underwent a regional evolutionary radiation of the genus *Sivalhippus* (Wolf et al. 2013). The oldest occurring member of the *Sivalhippus* clade is *Sivalhippus nagriensis* which occurred 10.5-9.3 Ma. The very large and very robust species *Sivalhippus theobaldi* ranged in age from 9.3 to 7.8 Ma. The large and robust species, *Sivalhippus perimensis* ranged in age from 8.5-7.3 Ma. The last locally occurring Potwar Plateau species, also large, *S. anwari* ranged from 7.4-7.2 Ma. In China, *Sivalhippus* cf. *theobaldi* is reported from Yunan, ca. 8.2-7.2 Ma (Sun 2013). *Sivalhippus ptychodus* occurred in Qingyang, Gansu ca. 7 Ma, and in Yushe and Wuxiang Basins, Shanxi in 7-6.5 Ma. *Sivalhippus platyodus* also occurred in the Yushe and Wuxiang Basins, Shanxi in 7-6.5 Ma and the Wulanhua area circa 7 Ma. *Sivalhippus* cf. *theobaldi* occured in Myanmar ca. 8 Ma and Yuanmou and Lufeng, Yunnan, China between 8 and 7 Ma (Qi et al. 2006; Sun 2013). Flynn and Qi (1982) argued the age of Lufeng fauna was 8 Ma. *Sivalhippus* also occured in Africa: in Uganda *S. macrodon* is circa 9 Ma, and is likely related to Siwalik *S. theobaldi*; *S. turkanensis* occurs at Lothagam, ca. 6.5 Ma (Bernor & Harris 2003) and plausibly Sahabi, circa 7 Ma (Bernor et al. 2010) and is related to *Sivalhippus perimensis* (Fig. 13).The phylogenetic analysis of Wolf et al. (2013) hypothesized that *S. platyodus* was the sister taxon of Siwalik *S. theobaldi*. However, we believe that eventhough the type specimen of Siwalik *S. nagriensis* is fragmentary, it is morphologically closer to *S. platyodus* than either *S. theobaldi* or *S. ptychodus*. Both *S. nagriensis* and *S. platyodus* have dorsoventrally extensive, subtriangular POF placed close to the facial-maxillary crest. We believe that at least these two species share a very close relationship. On the other hand, *S. ptychodus* is most similar to Siwalik *S. perimensis*. Although *S. ptychodus* and *S. platyodus* have overlapping geographic and choronologic distributions in China, they likely represent two separate dispersal events of hipparion horse from Indopakistan (Fig. 13).

## Conclusions

*Sivalhippus ptychodus* has derived features including a long POB, strongly developed POF placed dorsally high and far anteriorly shallow nasal notch, complexly plicated upper cheek tooth fossettes, lingually flattened and labially rounded protocones, variably occurring pli caballinids, rounded to triangular metaconids, triangular metastylid and broad

U-shaped linguaflexid on the mandibular molars typical for the genus *Sivalhippus*. *Sivalhippus ptychodus* differs from *S. platyodus* in having a POF placed high on the face with a shorter POF dorsoventral height. *Sivalhippus ptychodus* is a valid species and not a synonym of *S. platyodus*. The facial morphology of *S. ptychodus* most resembles that of Siwalik *S. perimensis* and to a limited extent, *S. turkanensis*, whereas that of *S. platyodus* is more similar to *Sivalhippus nagriensis*. *Sivalhippus* spp. likely extended its range from South Asia into China between 9 and 7 Ma.

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## Appendix

### 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 absent; G = 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.

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.

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 = strong, 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.

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) Presence of dP1: A = persistent and functional; B = reduced and non-functional; C = absent.

17) P2 anterostyle: A = short; B = elongate

18) Curvature of maxillary cheek teeth: A = very curved; B = moderately curved; C = straight.

19) Maximum cheek tooth crown height: A = < 30 mm; B = 30 - 40 mm; C = 40 - 60 mm; D = 60 - 75 mm; E = 75+ maximum crown height.

20) 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.

21) Confluence (linkage) of pre- and postfosstte opposing

borders: A = linked; B = separate.

22) Posterior wall of postfossette: A = may not be distinct; B = always distinct.

23) Pli caballin morphology: A = double; B = single or occasionally poorly defined double; C = complex; D = plis not well formed.

24) Hypoglyph: A = hypocone frequently encircled by hypoglyph; B = deeply incised, infrequently encircled hypocone; C = moderately deeply incised; D = shallowly incised.

25) 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.

26) Protocone flattened: A = yes; B = no

27) Isolation of protocone: A = connected to protoloph; B = isolated from protoloph.

28) Protoconal spur: A = elongate, strongly present; B = reduced; C = absent.

29) Premolar protocone/hypocone alignment (pre- Old World hipparionine condition): A = anteroposteriorly aligned; B = protocone more lingually placed.

30) Molar protocone/hypocone alignment (pre- Old World hipparionine condition): A = anteroposteriorly aligned; B = protocone more lingually placed.

31) p2 anterostylid: A = elongate; B = short and rounded.

32) Mandibular incisor morphology: A = not grooved; B = grooved.

33) Mandibular incisor curvature: A = curved; B = straight.

34) I3 lateral aspect: A = elongate, not labiolingually constricted; B = very elongate, labiolingually constricted distally; C = atrophied.

35) Premolar metaconid: A = rounded; B = elongated; C = angular on distal surface; D = irregular shaped; E = square shaped; F = pointed.

36) Molar metaconid: A = rounded; B = elongated; C = angular on distal surface; D = irregular shaped; E = square shaped; F = pointed.

37) Premolar metastylid: A = rounded; B = elongate; C = angular on mesial surface; D = irregular shaped; E = square shaped; F = pointed.

38) Premolar metastylid spur: A = present; B = absent

39) Molar metastylid: A = rounded; B = elongate; C = angular on mesial surface; D = irregular shaped; E = square shaped; F = pointed.

40) Molar metastylid spur: A = present; B = absent

41) Premolar ectoflexid: A = does not separate metaconid and metastylid; B = separates metaconid and metastylid.

42) Molar ectoflexid: A = does not separate metaconid and metastylid; B = separates metaconid and metastylid; C = converges with preflexid and postflexid to abut against metaconid and metastylid.

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

44) 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.

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

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

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

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

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

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

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

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