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The first occurrence of *Eurygnathohippus* Van Hoepen, 1930 (Mammalia, Perissodactyla, Equidae) outside Africa and its biogeographic significance

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KEY WORDS - South Asia, Pliocene, Biogeography, Dispersal, Siwalik, Hipparionine horses.

*ABSTRACT - The Pliocene fossil record of hipparionine horses in the Indian Subcontinent is poorly known. Historically, only one species, "*Hippotherium*"* antelopinum *Falconer & Cautley, 1849, was described from the Upper Siwaliks. Here, we present the first evidence of* Eurygnathohippus *Van Hoepen, 1930, a lineage hitherto only known from Africa, in the Upper Siwaliks during the late Pliocene. Morphologically, the South Asian* Eurygnathohippus *is most similar to* Eurygnathohippus hasumense *(Eisenmann, 1983) from Afar, Ethiopia, a species with a similar temporal range.* Eurygnathohippus *appears to have dispersed into South Asia from the west via the Levantine Corridor and the Middle East in the early Pliocene. The presence of this lineage in the Indian Subcontinent refines our understanding of equid evolution and biogeography in the region.*

RIASSUNTO - [Il primo ritrovamento di *Eurygnathohippus* Van Hoepen, 1930 (Mammalia, Perissodactyla, Equidae) fuori dal continente africano e il suo significato biogeografico] *- Il registro pliocenico dei cavalli ipparionini per il Subcontinente Indiano è scarsamente conosciuto. Storicamente è nota una sola specie, "*Hippotherium*"* antelopinum *Falconer & Cautley, 1849, descritta in località degli Upper Siwaliks. Gli autori di questo contributo hanno recentemente segnalato la presenza dell'ipparionino cinese* Plesiohipparion huangheense *(Qiu et al., 1987) nel Pliocene superiore dell'India. In questo contributo viene presentata la prima evidenza della presenza di un'altra specie di cavallo ipparionino,* Eurygnathohippus *Van Hoepen, 1930, nel Pliocene superiore degli Upper Siwaliks. Il genere* Eurygnathohippus *sino ad oggi era conosciuto esclusivamente nel Continente Africano. I resti di* Eurygnathohippus *qui descritti provengono dai Siwaliks indiani e dal Potwar Plateau in Pakistan. La presenza di ectostilidi e piega caballinide su denti mandibolari ha consentito di attribuirli con certezza al genere* Eurygnathohippus*. Da un punto di vista morfologico, il rappresentante sud asiatico di* Eurygnathohippus *è particolarmente simile a* Eurygnathohippus hasumense *(Eisenmann, 1983) approssimativamente coevo e proveniente dalla regione Afar, in Etiopia.* Eurygnathohippus *sembra quindi essere andato incontro a un evento di dispersione verso il sud est asiatico attraverso il Corridoio Levantino e il Medio Oriente. La presenza di questo genere nel Subcontinente Indiano migliora la nostra comprensione della storia evolutiva degli equidi e la biogeografia della regione.*

INTRODUCTION

The North American hipparionine horse *Cormohipparion* Skinner & MacFadden, 1977 extended its range to Eurasia between 11.4 and 11.0 Ma, appearing in Africa slightly later (Woodburne & Swisher III, 1995; Woodburne, 2007, 2009; Bernor & White, 2009; Bernor et al., 2017). Thereafter, Old World hipparionine horses underwent two major evolutionary radiations, one in the late Vallesian-early Turolian (MN9-MN11, ca. 11.2-8.7 Ma) and the other, later in the latest Miocene-Pleistocene (MN13-MQ2, 7.1-0.5 Ma; Bernor et al., 1996, 2010; Wolf et al., 2013). The initial Old World radiation included lineages of *Hippotherium* Kaup, 1833*, Cremohipparion* (Qiu et al., 1987)*, Hipparion* s.s. de Christol, 1832, *Baryhipparion* (Qiu et al., 1987) and *Sivalhippus* Lydekker, 1877 (Bernor et al., 1996, 2010). The later radiation would appear to have emerged from South Asian *Sivalhippus* (Bernor & Hussain, 1985; Wolf et al., 2013) and included "*Sivalhippus* Complex" taxa-*Eurygnathohippus* originating in Africa, *Proboscidipparion* Sefve, 1927 in East Asia, and *Plesiohipparion* (Qiu et al., 1987), originating in China and later dispersing throughout Eurasia (Qiu et al., 1987; Bernor et al., 1996, 2010; Jukar et al., 2018).

The genus *Eurygnathohippus* is first recorded from the latest Miocene of Africa in Lothagam, Kenya (Bernor & Harris, 2003), Middle Awash, Ethiopia (Bernor & Haile-Selassie, 2009) and Sahabi, Libya (Bernor et al., 2012). Until now, *Eurygnathohippus* was thought to be an endemic African lineage (Bernor et al., 2010). These horses are characterised by the persistent presence of ectostylids and pli caballinids on adult mandibular cheek teeth. While pli caballinids and ectostylids are found on the earliest occurring Old World hipparions from the Vienna Basin, *Hippotherium* sp., they rarely persist in early Vallesian Central European members of *Hippotherium* and are weakly developed and do not rise high on the labial aspect of the permanent cheek tooth dentition (Bernor et al., 2017). All other hipparionine lineages lost

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the ectostylids on the permanent cheek teeth except for African *Eurygnathohippus*. We report here specimens of *Eurygnathohippus* sp. from the late Pliocene (3.6-2.58 Ma) of the Upper Siwaliks of India and Pakistan. The presence of this taxon in the Upper Siwaliks represents a Pliocene dispersal event from East Africa, through the Middle East, and into South Asia.

MATERIALS AND METHODS

Specimens

Herein, we examine specimens from the South Asian Siwaliks, and Ethiopia. The South Asian specimens studied here are WIF/A 124, PUA/SK-07/81, and SFP 73 (formerly GSI 21019 [GSI = Geological Survey of India]) from NW India, and NHMUK PV M. 100347 (formerly BMNH M.15396) from the Potwar Plateau in NE Pakistan. WIF/A 124 is curated at the Wadia Institute of Himalayan Geology, Dehra Dun, India (WIF/A), PUA/SK-07/81 is curated in the Department of Anthropology, Panjab University, Chandigarh, India (PU), SFP 73 is curated at the Siwalik Fossil Park, Saketi, India (SFP), and NHMUK PV M. 100347 is curated in the Department of Earth Sciences, Natural History Museum, London (NHMUK). The Ethiopian mandibular m1s cited herein (Tab. 1) have been referred to *Eurygnathohippus hasumense* by Bernor et al. (2010) and are housed at the National Museum of Natural History, Addis Ababa, Ethiopia (AL) and are relevant for size comparison only; measurements on teeth alone have limited taxonomic value. All measurements were taken using digital calipers to the nearest 0.1 mm.

GEOLOGICAL FRAMEWORK

The Siwalik specimens described herein come from late Pliocene sediments on the Potwar Plateau in Pakistan and the Siwalik Hills in NW India (Fig. 1a-b). These are fluvial deposits ranging in age from 3.6-2.58 Ma (Kumar & Tandon, 1985; Willis, 1993; Sangode & Kumar, 2003; Kumaravel et al., 2005). WIF/A 124 was collected ~400 m ENE of the village of Dulopur (30°40’32”N, 77°00’36”E) (Fig. 1c). The Siwalik sediments here are exposed east of the Sabilpur fault, and along an anticline, the southern limb of which is truncated by Himalayan Frontal Thrust

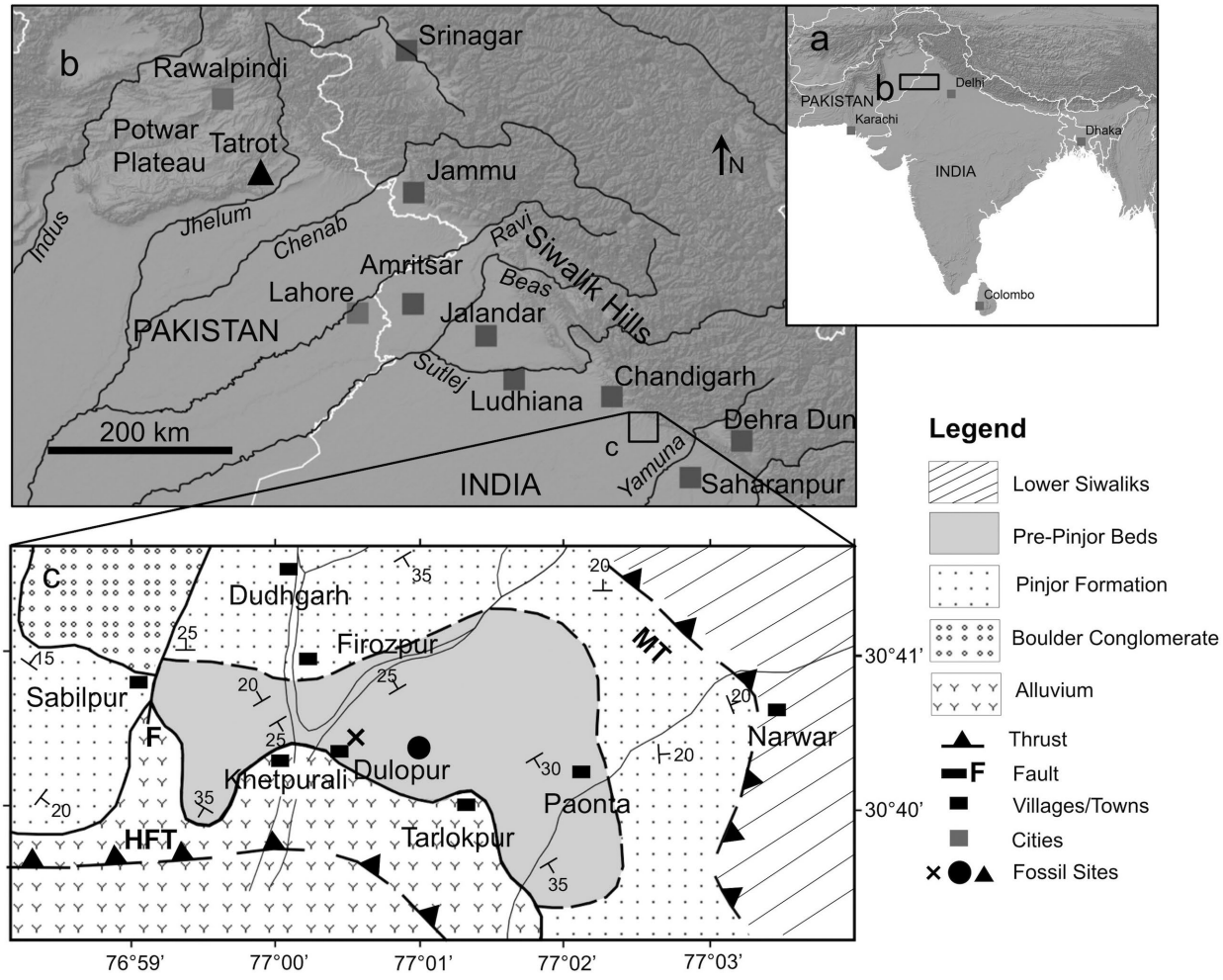

Fig. 1 - Location map showing the sites where *Eurygnathohippus* sp. specimens have been found in the Siwaliks. a) Study area within the Indian Subcontinent. b) Localities for NHMUK PV OR M.100347 (black triangle) and WIF/A 124, WIF/A 114, and PUA/SK-07/81 (square boxes) in relation to the major cities and rivers in northern Indo-Pakistan. c) Zoomed in view of the area showing the sites where WIF/A 124, WIF/A 114 (black “×”), and PUA/SK-07/81 (black circle) were found. HFT, Himalayan Frontal Thrust; MT, Markanda Thrust.

(Nanda, 1981). Pliocene strata are exposed in the center of the anticline, and are 200 m thick on the northern limb (Nanda, 1981). The Pliocene sediments consist of fine to medium grained grey to variegated mudstones and grey and brown sandstones, and have been dated magnetostratigraphically on the northern limb to 3.3-2.58 Ma (Tandon et al., 1984). PUA/SK-07/81 was collected in the same vicinity of WIF/A 124, ~500 m east of the village of Khetpurali (30° 40' 35.86''N, 76° 59' 57.08''E) from a grey sandstone layer (Fig. 1c; Kumar et al., 2014). NHMUK PV M. 100347 is part of the H.M. Sale collection presented by the Burmah Oil Company to the Natural History Museum, London. This tooth was collected near Tatrot (33° 1' 26.76''N, 73° 47' 32.20''E) on the Potwar Plateau, the type locality of the Tatrot Formation (Fig. 1b). This 60 m thick fossiliferous section consists of sandstones and mudstones, and lies unconformably with a hiatus of about 2 Ma on top of Middle Siwalik exposures (Opdyke et al., 1979; Barry et al., 1982). Locally, the Tatrot Formation has been estimated to date to 3.5-3.2 Ma (Barry et al., 2013). The last specimen SFP 73 comes from an unknown locality in the Indian Siwaliks, most probably late Pliocene in age.

SYSTEMATIC PALAEONTOLOGY

Order Perissodactyla Owen, 1848
Suborder Hippomorpha Wood, 1937
Superfamily Equoidea Hay, 1902
Family Equidae Gray, 1821
Subfamily Equinae Steinmann & Döderlein, 1890
Tribe Hipparionini Quinn, 1955

Genus *Eurygnathohippus* Van Hoepen, 1930
Type species *Eurygnathohippus cornelianus* Van Hoepen, 1930

Eurygnathohippus sp.
(Fig. 2a-d)

Referred Specimens - WIF/A 124, PUA/SK-07/81, NHMUK PV M. 100347, SFP 73.

Locality and Horizon - These specimens come from the late Pliocene (3.6-2.58 Ma) beds of the Siwalik Group in India and Pakistan. For more details, see the Geological Framework.

Diagnosis (modified from Bernor et al., 2010) - *Eurygnathohippus* is a genus of hipparion that varies in size from large to small; preorbital fossa poorly developed to absent; maxillary cheek teeth with dP1 strongly reduced or absent; cheek tooth crown height may reach 90 mm in the most advanced African Pleistocene members; cheek tooth pre- and postfossettes are moderately complex; protocones usually oval; mandibular metaconid and metastylid generally rounded to square but may become pointed especially in more advanced species; linguaflexid usually broad; U-shape preflexids and postflexids have enamel margins that vary in their complexity; pli caballinids usually persistent; ectostylids evolve from small low crowned, small and rounded structures to larger high crown structures with increased length and width from base to crown occlusal surface; in advanced African members, incisors become hypertrophied and procumbent with I3/i3 strongly reduced in advanced, later species. Metapodial IIIs and 1st Phalanges III vary from being robust to slender built.

Description - WIF/A 124 is a moderately worn adult left first mandibular molar (m1; Fig. 2a1-2, Tab. 1). The pli caballinid is strongly developed. Figure 2 a1 shows that the metaconid is rounded/elongate whereas the metastylid is square shaped and has a metastylid spur; preflexid is elongate but restricted labio-lingually near its mesial limit; postflexid is elongate with complexity at its mesial end.

NHMUK PV M. 100347 is a third or fourth mandibular premolar (p3 or p4) from the Tatrot faunal zone of the Potwar Plateau, Pakistan (Fig. 2b1-2, Tab. 1). This specimen shows a remarkable resemblance to WIF/A 124 in its rounded metaconid, squared metastylid (with some lingual pointing), small but distinct pli caballinid and ectostylid. Forsten (1997) referred this specimen to "the caballoid enamel pattern of *Plesiohipparion rocinantis*", and did not recognise its affinity to the "eurygnathohippine" (her terminology) clade of a p4-m1 from the Vogel River, Tanzania described by Dietrich (1942).

PUA/SK-07/81 is a worn third mandibular molar (m3) collected approximately 5 kilometers west of the Dolupur specimen (Fig. 2c1-2, Tab. 1). Kumar et al. (2014) erroneously described this specimen as being a small subspecies of *Equus*, *E. sivalensis minor* Gaur & Chopra, 1984. This specimen has an occlusal length of 27.1 mm, width (M8) of 8.2 mm, and a crown height of 46.5 mm (measurement key from Bernor et al., 1997). Metaconid is rounded/elongate, metastylid is square; preflexid and postflexid are elongate with simple margins; pli caballinid is distinct and ectostylid can be discerned on both the occlusal and labial views (Fig. 2c1-2). Along with the aforementioned characteristics, the lack of a strongly developed mesio-labially directed pli on the preflexid also suggests an affinity with *Eurygnathohippus* sp. rather than *Equus.*

SFP 73 (formerly GSI 21019) is a left p4 of uncertain provenance from the Indian Siwaliks (Mishra et al., 2013). Dimensions of this tooth are: length = 26.4 mm, width = 13.7 mm and height = 41.5 mm. As with the previously described specimens, metaconid is rounded, metastylid is square-shaped, preflexid has simple margins while postflexid exhibits some complexity of its labial margin. Pli caballinid is distinctly developed and ectostylid is large, elongate with a large mesially directed pli. The ectostylid is larger and more developed than the other three specimens (Fig. 2d).

Remarks - WIF/A 124, was first described as *Hipparion* sp. by Nanda (1979). This diagnosis was revised by Nanda (2015) to ?*Hipparion antelopinum*. However, the presence of the prominent pli caballinid and the well-developed ectostylid are diagnostic of the genus *Eurygnathohippus*. WIF/A 124 shows a remarkable resemblance to Hadar, Ethiopia mandibular m1s (Tab. 1 of the Supplementary Online Material). NHMUK PV M. 100347 and PUA/

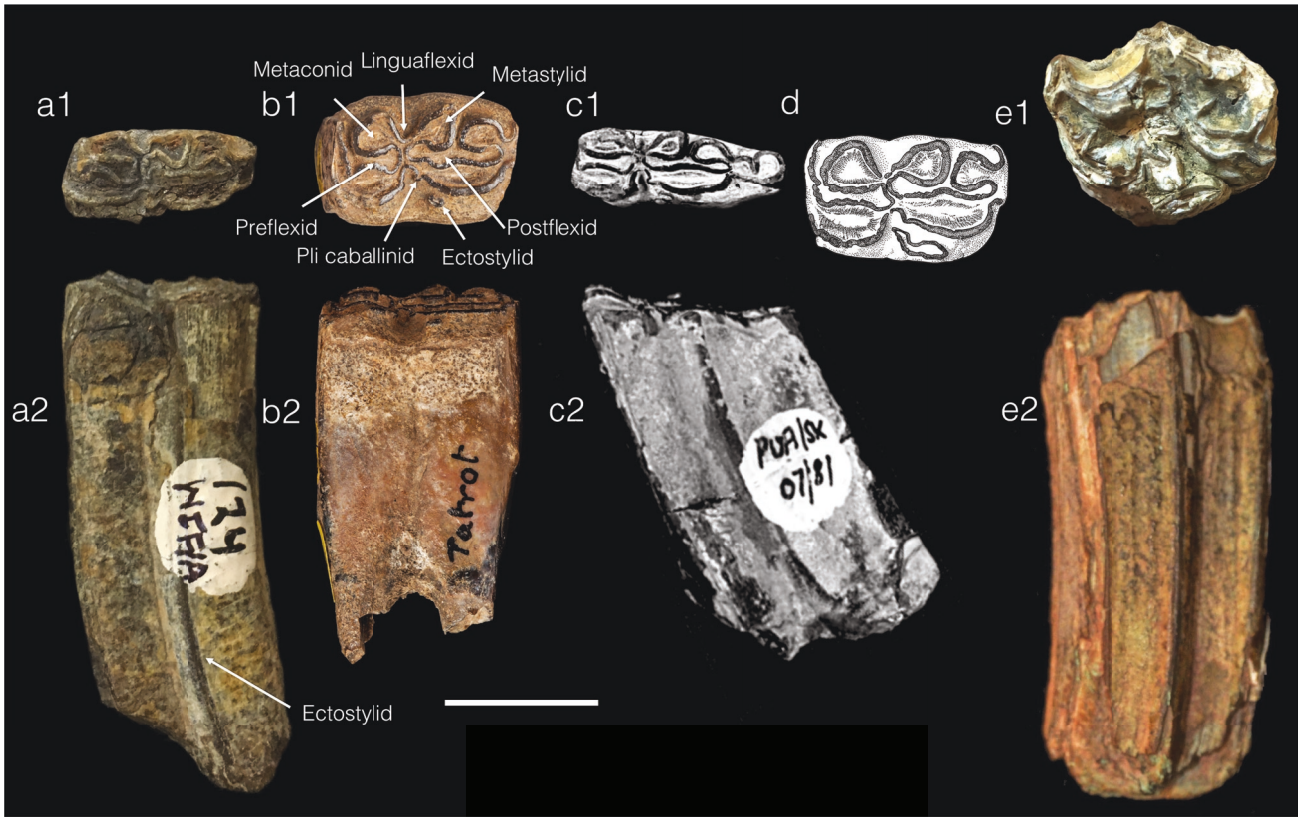

Fig. 2 (color online) - Comparison of the four mandibular teeth of *Eurygnathohippus* sp. (a-d) and one maxillary tooth of ?*Eurygnathohippus* sp. (e) from the Siwaliks of South Asia. a1-2) Occlusal and labial view respectively of WIF/A 124 (m1). b1-2) Occlusal and labial view respectively of NHMUK PV OR M.100347 (p3/p4). c1-2) Occlusal and labial view respectively of PUA/SK-07/81 (m3) modified and reproduced from Kumar et al. (2014) with publisher's permission. d) Occlusal line drawing of SFP 73 (p4), original image in Mishra et al. (2013). e1-2) Occlusal and lingual view respectively of WIF/A 114 (P3/P4). Scale bar is equal to 20 mm.

SK-07/81 are very similar to WIF/A 124, particularly in their development of metaconid, metastylid, plicaballinid and ectostylid.

Table 1 provides a comparison of measurements on 44 m1s from Hadar, Ethiopia compared to WIF/A 124, NHMUK PV M. 100347, PUA/SK-07/81 and SFP 73. Bernor et al. (2010) referred the Hadar specimens to *Eurygnathohippus hasumense*. These range in age from 3.4 to 2.9 Ma. The Siwalik specimens overlap the range of all Hadar *E. hasumense* measurements except for the four width measurements (M6-M9) for which it is slightly smaller. The crown height (M10) of WIF/A 124 is only slightly less (61.0 mm) than the maximum crown height for Hadar *E. hasumense* m1 (64.5 mm) which is remarkable since the WIF/A 124 is not in early wear. Ectostylid length of WIF/A 124, NHMUK PV M. 100347 and PUA/SK-07/81 (2.1-3.7 mm) is the lower part of the range of *E. hasumense* (2.4-7.4 mm). Ectostylid height

Specimen	Element	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13
Hadar Specimens	m1	22.1 31.5	20.6 29.1	11.6 17.3	5.8 10.7	6.3 14.9	11.9 19.5	13.2 15.9	9.6 15.6	9.6 15.7	23.5 64.5	2.4 7.4	1.4 3.6	23.3 61.6
WIF/A 124	m1	25.5	23.1	13.7	7.5	11.6	11.3	11.7	9.3	9.0	61.0	3.7	na	46.8
PUA/SK-07/81	m3	27.1	24.3	13.2	7.9	11.3	10.1	na	8.2	8.5	46.5	2.1	1.1	36.1
NHMUK PV M. 100347	p3/p4	24.1	23.9	13.8	7.8	12.8	16.6	11.3	13.1	11.0	34.2	2.4	1.8	25.1
SFP 73	p4	26.4	21.8	16.5	9.6	12.7	16.4	na	13.7	12.7	41.5	5.9	2.1	na

Tab. 1 - Mandibular dental measurements (in mm) for *Eurygnathohippus* sp. from the Siwaliks, and *Eurygnathohippus hasumense* from Hadar. The measurements for the Hadar specimens represent the range of variation with the upper number being the minimum measurement, while the lower number is the maximum. Raw data for these specimens is given in Tab. 1 of the Supplementary Online Material. M1 = length at occlusal level; M2 = length 10 mm above the tooth's base; M3 = length of metaconid-metastylid; M4 = length of the prefossette; M5 = length of the postfossette; M6 = width across plane of ectoflexid/linguaflexid; M7 = width 10 mm above the tooth's base; M8 = width across plane of metaconid and enamel band labial to protoconid; M9 = width across plane of metastylid and enamel band labial to hypoconid; M10 = crown height as measured from base to occlusal level on mesial face of the tooth; M11 = ectostylid length; M12 = ectostylid width; M13 = ectostylid height.

of the highest crowned Siwalik specimen, WIF/A 124 (46.8 mm) is less than the maximum for *E. hasumense* (61.6 mm). SFP 73 clearly differs from the other three specimens and the Hadar sample in having a larger, more elongate ectostylid. It is possible that this specimen of *Eurygnathohippus* is younger than the other three. However, the ectostylid is also similar in morphology to those from Vogel River *Eurygnathohippus* specimens described by Dietrich (1942, pl. 13, fig. 91).

In all four of these specimens, the co-occurrence of an ectostylid rising high on the labial side of the crown accompanied with a strongly developed pli caballinid is diagnostic of an advanced Pliocene species of *Eurygnathohippus*. Bernor et al. (2017) discovered that weakly developed pli caballinids and ectostylids that do not rise high on the crown are diagnostic of the oldest and most primitive hipparions referred to *Hippotherium* sp. from the Vienna Basin. Small, weakly developed ectostylids with pli caballinids are known from the latest Miocene of Kenya, Ethiopia and Libya *Eurygnathohippus* (Bernor & Harris, 2003; Bernor & Haile-Selassie, 2009; Bernor et al., 2010, 2012). The first well-developed ectostylids that rise moderately high on the labial wall of the crown are known from 4.4 Ma horizons from Aramis, Ethiopia (Bernor et al., 2013). Subsequent to the late Pliocene African hipparions, African *Eurygnathohippus* evolved higher crowned cheek teeth with ectostylids rising higher on the crown and becoming longer and wider occlusal features. Our close comparison of the 3.6-2.9 Ma Hadar *Eurygnathohippus hasumense* correlates closely with the Siwalik molars described herein. However, accompanying complete metapodial IIIs would be needed to confirm species identity to *Eurygnathohippus hasumense*. If indeed SFP 73 is a more advanced hipparionine, as it would appear, this form shows intriguing similarity to *Eurygnathohippus pomeli* (Eisenmann & Geraads, 2007) from the earliest Pleistocene of Morocco (Eisenmann & Geraads, 2007). However, this cannot be confirmed until the provenance of SFP 73 is ascertained or other similar specimens are found in a chrono-stratigraphic context.

DISCUSSION

Bernor et al. (1996) recognised the *Sivalhippus* Complex to include the genera *Sivalhippus*, *Eurygnathohippus*, *Plesiohipparion* and *Proboscidipparion. Sivalhippus* appears to have originated in South Asia, diversified and radiated in the late Miocene (Wolf et al., 2013). Sun et al. (2018) have recently reported that *Sivalhippus* not only extended its range into Africa in the late Miocene (*Sivalhippus macrodon* Eisenmann, 1994 and *Sivalhippus turkanensis* Hoojier & Maglio, 1974; Bernor et al., 2010; Wolf et al., 2013) but also into China where two species are recognised, *Sivalhippus platyodus* (Sefve, 1927) and *Sivalhippus ptychodus* (Sefve, 1927). *Eurygnathohippus*, *Plesiohipparion*, and *Proboscidipparion* are sister taxa that likely arose as a group in the late Miocene, with the former initially becoming isolated in Africa (Bernor et al., 2010), while the latter two lineages arose in east Asia and extended their range into Turkey and Western Europe (Bernor & Sun, 2015; Bernor et al., 2015a, b). *Eurygnathohippus* retained and further evolved strongly developed pli caballinids and ectostylids, the latter structure being the most prominent and constant, distinguishing it from other sister taxa. The presence of this taxon in the Upper Siwaliks reveals a Pliocene range expansion of this lineage, and significantly impacts our understanding of equid diversity in the Indian Subcontinent.

The record of hipparionines is best resolved in the late Miocene of the Potwar Plateau in Pakistan where species of *Cormohipparion*, *Sivalhippus* and *Cremohipparion* are documented in the stratigraphic record from 10.8 to 6.3 Ma (Wolf et al., 2013). In comparison, Pliocene hipparionine occurrences are isolated on the Indian Subcontinent. Historically, only one species of hipparionine horse was described from the Upper Siwaliks, "*Hippotherium*" *antelopinum* Falconer & Cautley, 1849 (= *Cremohipparion antelopinum* [Wolf et al., 2013]). The lectotype of *Cremohipparion antelopinum* is NHMUK PV M. 2647 (originally BMNH M. 2647), a right maxillary fragment of a young adult with P2-M3 (MacFadden & Woodburne, 1982; Bernor & Hussain, 1985; Wolf et al., 2013). NHMUK PV M. 2647 was discovered by Falconer and Cautley in the 1830's and '40s from the Indian Siwaliks (Falconer & Cautley, 1849; Lydekker, 1886a). Specimens recovered from the Potwar Plateau in Pakistan and referred to this species are relatively rare and characterised by belonging to a small to medium sized equid, upper cheek teeth with rounded protocones, lower cheek teeth would have rounded metaconids and metastylid and would lack pli caballinids and ectostylids (Wolf et al., 2013). The Potwar Plateau specimens range from 8.8-6.3 Ma (Wolf et al., 2013). Based on our understanding of the geology and age of the Siwalik sediments in the area surveyed by Falconer and Cautley (Murchison, 1868), and modern chronostratigraphic surveys, the holotype of *C. antelopinum* and other specimens referred to this species come from late Pliocene deposits (3.6-2.58 Ma; Azzaroli & Napoleone, 1982; Tandon et al., 1984; Ranga Rao, 1993; Kumaravel et al., 2005), suggesting that the *Cremohipparion* lineage persisted through the late Miocene into the Pliocene of the Indian Subcontinent.

A reassessment of Pliocene hipparionine specimens has also revealed the presence of *Plesiohipparion huangheense* from the Indian Siwaliks, a species formerly known only from Northern China and Turkey (Jukar et al., 2018). This species differs from the above specimens of *Eurygnathohippus* sp. by the presence of a very broad linguaflexid accompanied by strongly lingually pointed metaconids and metastylids and a lack of ectostylids on the permanent cheek teeth. The presence of *Eurygnathohippus* and *Plesiohipparion* is evidence for the ecological replacement of the *Sivalhippus* lineage by lineages from Africa (*Eurygnathohippus*) and eastern Asia (*Plesiohipparion*) in the Pliocene, when grasslands were widespread throughout the Indian Subcontinent.

A number of authors have reported *Sivalhippus theobaldi* Lydekker, 1877 from Pliocene beds in the Upper Siwaliks (Nanda, 1979; Azzaroli & Napoleone, 1982; Agarwal et al., 1993; Mishra et al., 2013). Wolf et al. (2013) showed that the *Sivalhippus* lineage ranges from ~10.6 Ma to ~6.8 Ma, as there is no strong evidence for the persistence of this lineage beyond the latest Miocene. A second hipparionine tooth (maxillary third or fourth

premolar [P3/P4], WIF/A 114, Fig. 2 e1-2), from the same locality that WIF/A 124, was previously described as *Sivalhippus theobaldi* because of its large size and greater crown height than "*Hipparion*" *antelopinum* (Nanda, 1979, 2015). However, we can identify no conclusive evidence to refer WIF/A 114 to this taxon. Taxonomic affinity cannot be reasonably determined because maxillary cheek teeth show less certain diagnostic characters than mandibular cheek teeth. While the size of this maxillary cheek tooth (occlusal length = 30.5 mm, occlusal width = 28.9 mm, crown height along the mesostyle = 70.1 mm) is congruent with lower cheek teeth, and given that it is from the same locality as WIF/A 124, we can only cautiously refer WIF/A 114 to ?*Eurygnathohippus* sp.

The late Pliocene occurrence of *Eurygnathohippus* in the Indian Subcontinent is part of a greater faunal exchange with Africa that introduced several lineages of grazers and open habitat specialists. A grassland corridor stretching from Africa through Eurasia facilitated the dispersal of these taxa during the latest Neogene (Edwards et al., 2010; Strömberg, 2011; Kaya et al., 2018). Carbon isotopes from dental enamel and soil both show that between 6.0 and 1.0 Ma, C4 grasslands were well established in Siwalik ecosystems (Quade et al., 1993; Sanyal et al., 2010; Patnaik, 2015). Indeed, *Eurygnathohippus* became more hypsodont and evolved open-habitat specializations in the late Miocene (Bernor et al., 2012, 2013). The flat occlusal surface on the Siwalik specimens, and relatively high crowns support a grazing habit for this taxon.

Further support for this Pliocene dispersal comes from the faunal assemblage found associated with *Eurygnathohippus* in the Siwaliks. The Tatrot Formation on the Potwar Plateau (3.5-3.2 Ma) has produced a diverse fauna that consisted of both endemic forms, and immigrant African lineages. Proboscideans such as *Stegodon* Falconer, 1857, bovids such as *Proamphibos lachrymans* Pilgrim, 1939, *Leptobos* sp. Rütimeyer, 1877, and *Antilope subtorta* Pilgrim, 1937, suids like *Sivachoerus prior* Pilgrim, 1926, *Hippohyus* Falconer & Cautley, 1847a, *Potamochoerus* Gray, 1854, and *Sivahyus* Pilgrim, 1926, the anthracothere *Merycopotamus* Falconer & Cautley, 1847b, and the tragulid *Vishnumeryx daviesi* (Lydekker, 1886b) make up the endemic fauna (Barry et al., 1982; Barry, 1995; Barry, pers. comm., 2018). Lineages found at Tatrot that originate from African taxa include the elephantid *Elephas planifrons* Falconer & Cautley, 1845, hippotragines such as *Sivoryx sivalensis* (Lydekker, 1878), reduncines such as *Sivacobus palaeindicus* (Lydekker, 1885) (syn. *Vishnucobus paluticornis* [Lydekker, 1878]; Vrba et al., 2015), the hippo *Hexaprotodon sivalensis* Falconer & Cautley, 1836a, and possibly the suid *Kolpochoerus* Van Hoepen & Van Hoepen, 1932 (Barry et al., 1982; Barry, 1995; Barry, pers comm., 2018). *Sivacobus* Pilgrim, 1939 and *Sivoryx* Pilgrim, 1939 are also inferred to be grassland specialists based on the ecological preferences of extant Reduncini and Hippotragini (Bobe et al., 2002). Other taxa that are present at the *Eurygnathohippus* bearing localities of Dulopur and Khetpurali include the gomphothere *Anancus* Aymard, 1856, stegodontids *Stegodon insignis* (Falconer & Cautley, 1845) and *Stegodon bombifrons* (Falconer & Cautley, 1847c), camel *Camelus sivalensis* Falconer & Cautley, 1836b, suids *Hippohyus tatroti* Pilgrim, 1926 and *Potamochoerus palaeindicus* Pilgrim, 1926, and open-habitat antelopes such as *Gazella lydekkeri* Pilgrim, 1937 (Nanda, 1976, 1977, 1981, 1982; Kumar & Gaur, 2013a, b; Kumar et al., 2014). Given the post-Miocene dispersal barriers between East Africa and West Asia across the Red Sea (Fernandes et al., 2006), the most probable dispersal route for *Eurygnathohippus* is via North Africa east through the Levantine corridor, and through the Middle East into South Asia.

CONCLUSION

We report here the first recorded occurrences of *Eurygnathohippus* outside of Africa. After 4 million years of isolation in Africa, *Eurygnathohippus* clearly extended its range into late Pliocene aged horizons of the Indian Subcontinent. Whereas specimens WIF/A 124, NHMUK PV M. 100347, and PUA/SK-07/81 are very similar in their morphology, SFP 73 is more derived in the structure of its ectostylid, suggesting a possible younger age. The fact that there are no other reported occurrences of *Eurygnathohippus* outside of Africa other than the late Pliocene horizons of the Indian Subcontinent suggest a limited biogeographic connection for this clade.

SUPPLEMENTARY ONLINE MATERIAL

All the Supplementary data of this work are available on the BSPI website at:
http://paleoitalia.org/archives/bollettino-spi/

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