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Neogene–Quaternary Mammalian Paleobiogeography of the Indian Subcontinent: An appraisal



Rajeev Patnaik

CAS in Geology, Panjab University, Chandigarh 160014, India

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ABSTRACT

A biostratigraphic evaluation of the Indian subcontinent Neogene–Quaternary mammal genera at 1 Ma intervals reveals a strong correlation between faunal turnovers (first and last appearances and immigrations), diversity and major tectonic and climate-induced sea level and vegetation changes at 23–22, 20–18, 17–16, 15–14, 11–10, 9–8, 3–2 and 1–0 Ma. The Early Miocene collision of Afro-Arabian and Eurasian Plates, followed by the Middle Miocene Climate Optima and the presence of evergreen rainforests, most likely facilitated the dispersals into and out of the subcontinent from the west along the coast and included African proboscideans, primates, creodonts, thryonomyid rodents and Asian chalicotheres, rhinos, suids, anthracotheres, carnivores and murid rodents. The Late Miocene and Early Pleistocene cooler and drier conditions, the spread of grasslands and sea level drops may have influenced the exchange of African monkeys, Eurasian carnivores, bovids, equids, camelid, and South Asian suids, leporids and murids. Immigrations from the east (East and SE Asia) occurred mostly during the Miocene and involved primarily small mammals.

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R É S U M É

Une évaluation biostratigraphique des genres de mammifères néogènes et quaternaires du sous-continent Indien à intervalles d'1 Ma révèle une forte corrélation entre les *turnovers* fauniques (première et dernière apparitions et immigrations) et la diversité, les principaux changements tectoniques, de climat, en liaison avec le niveau de la mer, et de végétation à 23–22, 20–18, 17–16, 15–14, 11–10, 9–8, 3–2 et 1–0 Ma. La collision, au Miocène inférieur, des plaques Afro-Arabique et Eurasiennne, suivie, au Miocène moyen, par les optima climatiques et la présence de forêts pluvieuses à feuilles persistantes, ont très probablement facilité les dispersions vers et en dehors du sous-continent Indien, à partir de l'ouest, le long de la côte et inclus des proboscidiens, primates, créodontes, rongeurs thryonomyidés africains et des chalicothères, rhino, suidés, anthracocères, carnivores et rongeurs muroïdés asiatiques. Les conditions plus fraîches et plus sèches du Miocène supérieur et du Pléistocène inférieur, l'extension des prairies et les abaissements du niveau de la mer peuvent avoir influencé les échanges entre singes africains, carnivores, bovidés, équidés et camélidés eurasiens et suidés, léporidés et muridés sud-asiatiques. Les immigrations à partir de l'est (Asie du Sud et du Sud-Est) se sont produites surtout pendant le Miocène et ont concerné principalement de petits mammifères.

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E-mail address: rajeevpatnaik@gmail.com<http://dx.doi.org/10.1016/j.crpv.2015.11.004>

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1. Introduction

The Indian subcontinent is a part of the Oriental Biogeographic Province of Wallace (1876), which is separated from the adjoining Palaearctic Biogeographic Province by mountain chains and desert habitat to the west and major rivers to the east (Fig. 1). The fauna and flora of the Oriental Biogeographic Province thrive under an essentially monsoonal climatic regime. Over much of the Neogene, the tectonics and climate played a major role in shaping the Oriental landscape and influenced the distribution of its biota including mammals. Within this province, the Indian Subcontinent appears as a separate subregion as it is bounded in the north, northwest and northeast by the Himalayan, Sulaiman, Hindu Kush and Indo-Burmese mountain chain and in the south by the Indian Ocean.

The freshwater Neogene–Quaternary molasse deposits exposed all along the Himalayan foothills from Pakistan in the west to Assam in the north-east, known as the Siwaliks, preserve a continuous record of fossil mammals. Barry and Flynn (1989) and Barry et al. (1985; 1990; 1991) discussed faunal interchanges and turnover in the Neogene of the

Siwaliks and proposed essentially three major episodes: one between 22 and 18 Ma, the second between 15 and 13 Ma and the third around 9.5 Ma. On the then-used time scale Barry et al. (2002) revised their Late Miocene turnover pulses based on a better time resolution and suggested three short periods of elevated Late Miocene turnovers at 10.3, 7.8 and 7.3–7.0 Ma. Flynn and Wessels (2013) discussed the small mammal biogeography of this region and the connections with North and East Africa, Arabia and Anatolia during the Miocene time. With the revised chronology of the deposits of Sulaiman province, new facts about the pre-existing Oligocene fauna and the Earliest Miocene mammalian local occurrences in the subcontinent emerged (Antoine et al., 2013; Barry et al., 2013; Flynn et al., 2013). Much research has been focused on the Pakistan Neogene over the last three decades and in recent years a number of Neogene and Quaternary mammal-bearing sites of India have been geochronologically dated (Patnaik et al., 2009; Pillans et al., 2005; Sangode et al., 2003), allowing a better understanding of the first and last appearances of several mammalian genera and a better correlation with well dated mammal sites (Flynn et al., 2013; Patnaik,

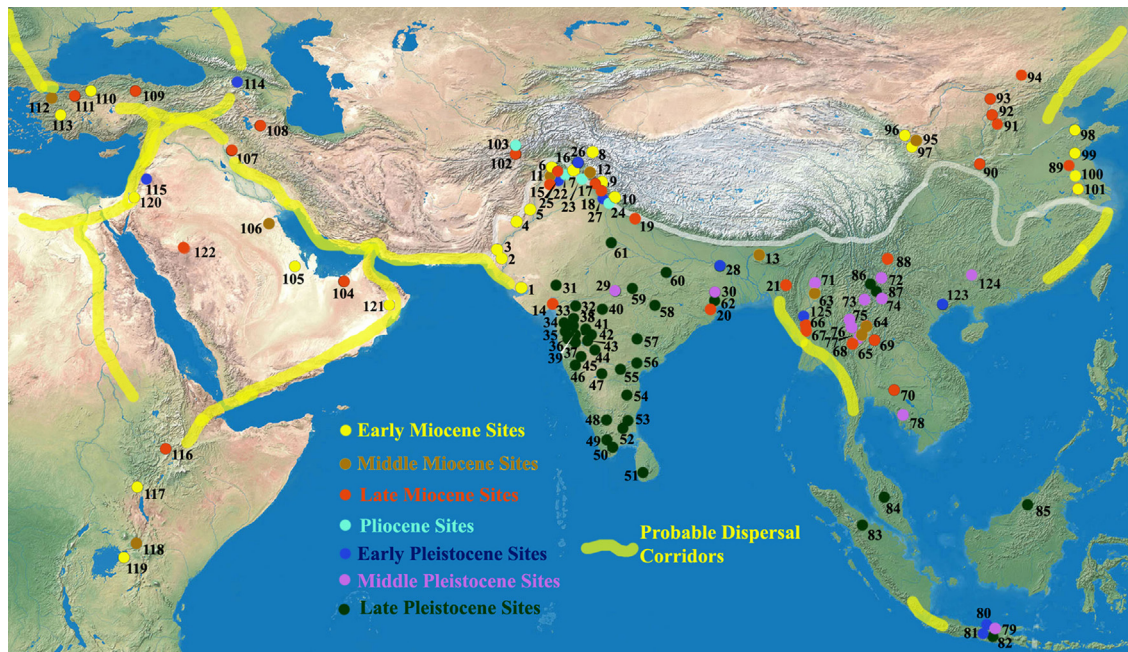


Fig. 1. Neogene–Quaternary mammal localities of the Indian subcontinent and other localities in the Oriental Province (south of the white line), Eurasia, Africa and Arabia with common elements. 1, Kutch; 2, Sehwan; 3, Gaj; 4, Bugti; 5, Zinda Pir; 6, Kamlial; 7, Kalakot; 8, Kargil; 9, Dharamsala; 10, Kasauli; 11, Chinji; 12, Ramnagar; 13, Garo Hills; 14, Perim Island; 15, Nagri; 16, Dhok Pathan; 17, Nurpur; 18, Haritalyangar; 19, Kalagarh; 20, Baripada Beds; 21, Boka Bill; 22, Tatro; 23, Parmandal; 24, Saketi; 25, Pabbi Hills; 26, Karewas; 27, Pinjor; 28, Bhagalpur; 29, Hathnora; 30, Kasai River; 31, Tajpur; 32, Tapi; 33, Nandur; 34, Manjra; 35, Godh; 36, Bori; 37, Chandoli; 38, Inamgaon; 39, Dhanegaon; 40, Purna; 41, Tadula; 42, Wangadari; 43, Ganjur; 44, Hagargundi; 45, Sirguppi; 46, Chikdauli; 47, Nittur; 48, Coimbatore; 49, Sayamalai; 50, Ayanaidipu; 51, Ratnapura; 52, Maruvattor; 53, Ariyalur; 54, Attirapakkam. 55, Kurnool Caves; 56, Venukonda; 57, Servaipet; 58, Mahanadi; 59, Narsighpur; 60, Son Valley; 61, Kalpi; 62, Bankura; 63, Chaungtha; 64, Mae Moh; 65, Chian Muan; 66, Yenangyaung; 67, Magway; 68, Li Mae Long; 69, Khorat; 70, Mun River sand Pits; 71, Mogok Caves; 72, Keo leng; 73, Tam Hang; 74, Tham OM; 75, Ban Fa Suai; 76, Khao Pah Nam; 77, Thum Wamin Nakin; 78, Phom Loang; 79, Kedung Brubus; 80, Trinil; 81, Ci Saat; 82, Punung; 83, Lida Ajer; 84, Kinta Valley; 85, Niah Cave; 86, Hang Hum; 87, Lang Trang; 88, Lufeng; 89, Laodong; 90, Bahe; 91, Yushe; 92, Lamagou; 93, Baode; 94, Ertemte; 95, Duitingou; 96, Zangjiaping; 97, Sigou; 98, Puzen; 99, Xeijiahe; 100, Sihong; 101, Fangsheng; 102, Khurdkabul; 103, Kabul; 104, Abudhabi (UAE); 105, Al Jadidah and Jabal miri ash Shamali; 106, As Sarrar; 107, Marageh, Iran; 108, Injana, Iraq; 109, Central and Western Anatolia; 110, Keskoy; 111, Sinap; 112, Pasalar; 113, Kargi, Kilcak and Harami, Turkey; 114, Dmanisi, Georgia; 115, Ubeidiya; 116, Chorora, Ethiopia; 117, Napak, Kenya; 118, Fort Ternan; 119, Rusinga; 120, Negev, Israel; 121, Ghaba, Oman; 122, An Nafud; 123, Sanhe, China; 124, Liujang Cave; 125, Irrawaddy Beds, Myanmar. Map source www.shadedrelief.com.

Fig. 1. Localités du sous-continent Indien comportant des mammifères du Néogène et du Quaternaire et autres localités de la province orientale (au sud de la ligne blanche), l'Eurasie, l'Afrique et l'Arabie, avec les éléments communs.

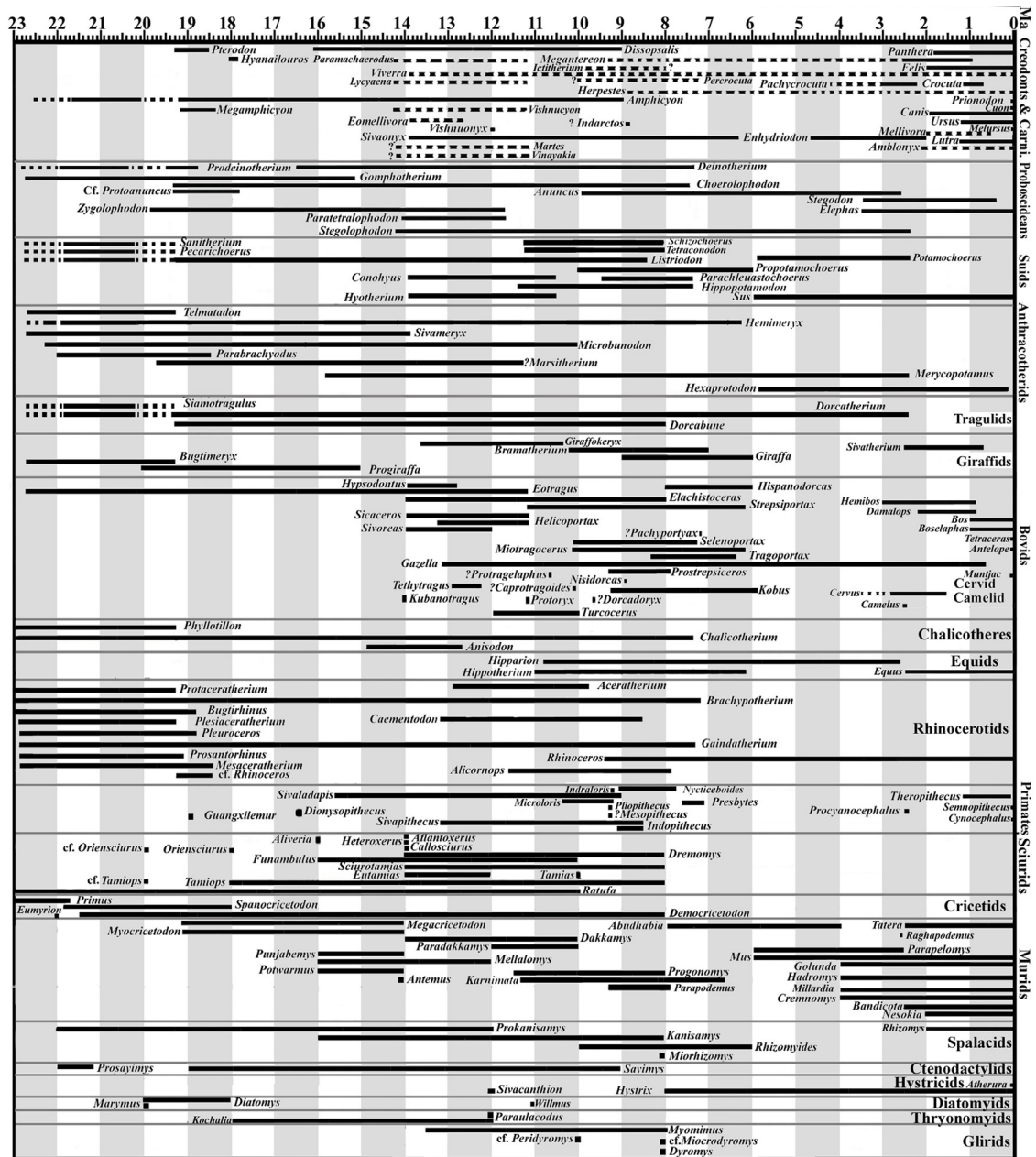


Fig. 2. Biostratigraphic ranges of various Neogene–Quaternary mammalian genera of the Indian subcontinent discussed here (data compiled from Antoine et al., 2013; Badgley et al., 2008; Barry et al., 2002, 2013, 2014; Flynn et al., 2013, 2014; Patnaik, 2013). Dashed lines indicate uncertain ranges.

Fig. 2. Intervalles biostratigraphiques de genres variés de mammifères néogènes–quaternaires du sous-continent Indien (données compilées à partir d’Antoine et al., 2013 ; Badgley et al., 2008 ; Barry et al., 2002, 2013, 2014 ; Flynn et al., 2013, 2014 ; Patnaik, 2013). Les lignes en tiretés indiquent les intervalles incertains.

2013). Furthermore, our understanding of paleoclimate and paleovegetation of the Indian subcontinent through the Neogene and Quaternary has also improved over the past decade or so. Therefore, the main goals of the paper are i) to re-evaluate the Neogene–Quaternary first and last appearances of various mammalian genera and to identify the number of dispersals into and out of the Indian subcontinent; and ii) to integrate these data with the available tectonic, climatic, vegetation and sea level data for western,

central and eastern Himalayan regions to understand whether there is any correlation between these biotic and abiotic events.

2. Methodology

The present assessment involves published records of Neogene and Quaternary mammals (mostly terrestrial) from various sites of the Indian subcontinent (Fig. 1),

at ~ 1 Ma time slices (Fig. 2). The data from Pakistan particularly between 18 and 5 Ma are well constrained paleomagnetically and geochronologically. Paleomagnetically and biochronologically dated sites from India, particularly those between 4.5 and 0.5 Ma are also fairly reliable and included in the NOW database (Fortelius, 2013). The data on diversity, first and last appearance dates (Fig. 2) and immigrant taxa come from the literature (Antoine et al., 2013; Badgley et al., 2008; Barry et al., 2002; Barry et al., 2013; Flynn et al., 2013; Flynn et al., 2014; Patnaik, 2013). Taxa that appeared in the subcontinent without any known ancestral lineage and with an older record in Africa, Eurasia or North, East and South-East Asia have also been considered immigrant. The lowest stratigraphic datum or the first local appearance of some taxa indicating the local record of oldest stratigraphic occurrence has been used following Flynn et al. (2013) and Antoine et al. (2013). Data are then used to make bivariate plots (Figs. 4, 5C). However, tentative age ranges of carnivores shown by dashed lines have not been used in this analysis. Finally the data sets have been integrated to decipher faunal turnovers, change in overall diversity and biogeographic connections within the oriental province (Myanmar, Indonesia, Thailand and South China) and outside (North China, West Asia, Europe, Arabia and Africa) (Figs. 4, 5).

3. Geological background

By the start of the Neogene, the Indian plate was firmly sutured to the Eurasian plate and the last remnant of the Tethys Sea retreated (Fig. 3). Around this time tectonic activity along the Main Central Thrust (MCT) in the central Himalayas and South Tibet Detachment System (STDS) in the western and eastern Himalayas (Catlos et al., 2001; Grujic et al., 2002; Yin, 2006) resulted in widespread exhumation (Clift et al., 2008). The northward movement of the Indian plate, followed by the gradual uplift of the surrounding terrain and the retreat of the Tethys, is archived in the sedimentary record exhibiting a transition from a shallow marine condition to an essentially fluvio-deltaic

environment in the Trans Himalayas (ex. Kargil deposits), Himalayan foreland basin (ex. Murrees) and Sulaiman Province of Pakistan. In the foreland basin this transition has been regarded by many as abrupt and representing a wide temporal gap (unconformity) amounting to the loss of most Oligocene sediment history (~ 10 Ma, Najman et al., 2004). In the Sulaiman Province of Pakistan, however, there is a consensus on the existence of some Oligocene (Lower Chitarwata Formation) fluvio-deltaic deposits yielding a wide variety of fossil mammals regarded as possible precursors to several Siwalik Miocene lineages (Antoine et al., 2013; Lindsay et al., 2005; Marivaux et al., 2005; Métails et al., 2009; Welcomme et al., 2001).

Around 18 Ma activation along the MCT in the eastern Himalayas and along the Great Counter Thrust (GCT) in the central and eastern Himalayas is noticed (Gansser, 1983; Harrison et al., 2000; Yin et al., 1999). Further uplift of the Himalayas and the Tibetan Plateau led to the development of mighty rivers such as the Indus and Ganges and their tributaries depositing the bulk of the molasse sediments into their respective foreland basins, and the rest was emptied into the Arabian Sea and the Bay of Bengal (Harrison et al., 1993). The Indus River flowed westward during Paleogene time (Downing and Lindsay, 2005; Métails et al., 2009). During the later part of the Early Miocene there was a major uplift of the Lesser Himalayas (Myrow et al., 2015), while the Lower Siwaliks were being deposited in the foreland basin. A large part of the western Gujarat was occupied by a shallow sea where terrestrial vertebrate remains were preserved in association with marine fauna in Kutch. At around this time Vihova Formation was also being deposited in the Sulaiman Province of Pakistan.

By the Middle Miocene, continued northward movement of the Indian Plate led to further crustal shortening and the rise of the Himalayas and sinking of the foreland basin in which thick piles of sediments were deposited by the Indo-Gangetic river systems. The floodplains were large and the conditions were warm and humid as indicated by thick paleosols and a diverse fossil rainforest flora (Srivastava et al., 2014 and references therein). Sediments belonging to overbank facies dominate compared to the channel facies, suggesting the presence of a meandering river pattern. At ~12 Ma tectonic activity along the Main Boundary Thrust (MBT) and STDS is noticed in the central and eastern Himalayas, respectively (Edwards and Harrison, 1997; Huyghe et al., 2001).

The Late Miocene is characterized by an increased rise of the Himalayas and intensification of the Asian monsoons (Amano and Taira, 1992; Harrison et al., 1993). The large emergent river system in northern Pakistan gave way locally to an inter-fan river system (Barry et al., 2002). At around 10 Ma, in northern India the fluvial architecture shows gradual changes from minor to major sandstone bodies, which in turn indicates an increase in the channel dimension there and the overall discharge with deposition taking place in large braided river system (Kumar et al., 2003). Around this time, the MCT resulted in reactivated high relief and increased supply of metamorphic detritus from the north. An alteration from a mudstone dominated to sandstone-dominated succession in the Siwaliks is time-transgressive, occurring at ~ 11 Ma in the Potwar Plateau,



Fig. 3. Hypothetical paleogeographic setting of the Indian subcontinent and probable dispersal routes of mammals during the Early Miocene ~ 20 Ma ago (modified after Métails et al., 2009; Fig. 4 B).

Fig. 3. Disposition paléogéographique hypothétique du sous-continent Indien et probables routes de dispersion des mammifères durant le Miocène inférieur voici ~ 20 Ma (d'après Métails et al., 2009, Fig. 4, modifié).

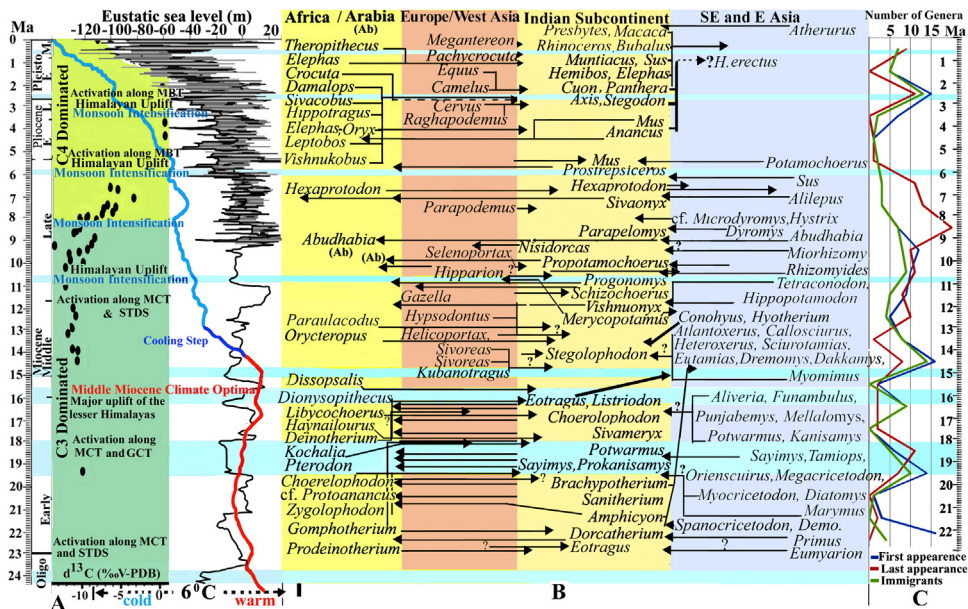


Fig. 4. A correlation between Neogene–Quaternary global temperature, sea levels and subcontinental tectonics and vegetation and mammalian faunal changes. A: Vegetation change based on mammalian enamel carbon stable isotope values (Martin et al., 2011 and references therein); eustatic sea levels (Miller et al., 2005) and temperature change (Zachos et al., 2001). B: Major dispersals of mammals to and from the Indian subcontinent. Broken lines: direction of dispersal not certain. C: Number of first and last appearances, and immigrants among the mammalian genera. Sky blue horizontal bands: Major drops in the sea level.

Fig. 4. Corrélation entre changements de température globale Néogène–Quaternaire, de niveaux marins et de tectonique subcontinentale, et de végétation et de faune mammalienne. A : Changement de végétation basé sur les valeurs de carbone stable sur l'émail de mammifère (Martin et al., 2011 et références incluses), de niveaux marins eustatiques (Miller et al., 2005) et du changement de température (Zachos et al., 2001). B : Dispersions majeures vers et à partir du sous-continent Indien. Lignes brisées : direction de dispersion incertaine. C : Nombre de premières et dernières apparitions et d'immigrants parmi les genres de mammifères. Bandes horizontales bleu ciel : énormes abaissements du niveau de la mer.

~ 10 Ma in Kangra sub-basin of India and ~ 9 Ma in Nepal (Kumar et al., 2003). 11–9 Ma saw an increase in sedimentation rate throughout the foreland basin (Kumar et al., 2003). At ~ 5.9 Ma a reactivation of MCT in the western and central Himalayas occurred (Catlos et al., 2002) and forests declined, giving way to grasslands as indicated by stable carbon and oxygen isotopes of soil concretions, palynological and mammalian enamel studies (Cerling et al., 1997; Hoorn et al., 2000). Sedimentological evidence also indicates an increase in drier and more seasonal conditions in Pakistan (Barry et al., 2002) (Fig. 4A).

Early Pliocene tectonic activity resulted in the deposition of thickly bedded conglomerate facies with lensoid bodies of sandstone and mudstones. At ~ 5.3 Ma MBT reactivates in the Simla Himalayas (Najman et al., 2004). Around 5 Ma, the progradation of conglomerate in the Dehradun sub-basin (Kumar et al., 2003) and western Himalaya indicates river reorganization (Clift and Blusztajn, 2005). In the Jammu and Chandigarh regions, fine-grained facies belong to the Tatrot and Pinjor formations. Tectonic activity along the MBT created an increased stream gradient, suggesting a broad catchment area with high basin relief, forcing the river system to deposit laterally coalescing megafans. This fluvial regime provided a high volume of sediment, depositing coarse-grained sediments in the proximal areas and the fine-grained ones in the distal part of the alluvial fan system (Kumar et al., 2003 and references therein).

The beginning of the Pleistocene saw intensified tectonic activity, caused mainly by movement along the MBT in the Himalayan foothills and MCT reactivated in the Nepal Himalayas at ~ 3.3 and ~ 2.4 Ma (Sorkhabi et al., 1996). Between 3 and 2 Ma sedimentation rates increase in the Subathu sub-basin (Kumar et al., 2003), with sediments deposited in the Bengal Fan (Metivier et al., 1999). This activity significantly altered the riverine system by increasing fan deposits in the piedmont regions and decreasing the flood plain deposits. Inter-fluvial flood plains were the areas where flora and fauna thrived, while fan deposits restricted the preferred habitat of large mammals. Siwalik paleosols indicate existence of warm and humid Early Pleistocene conditions followed by cool and dry conditions during the Middle Pleistocene (Sangode et al., 2001). Stable carbon and oxygen isotope studies of Siwalik palaeosols exposed near Haripur, India (Sanyal et al., 2010) indicated monsoon intensification at 11, 6 and 3 Ma (Fig. 4A).

4. Paleovegetation

In the Oligocene Chitarwata Formation of Sulaiman Province of Pakistan nearby mountains as high as 2000 m and a mixed vegetation (humid forests and dry open areas) is indicated by the presence of *Picea*, *Pinus*, *Cedrus*, *Betula*, *Alnus*, Fagaceae and *Quercus* (De Franceschi et al., 2008). Temperate broad leaf, *Terminalia* and *Palmae* suggest the presence of tropical rain forests (De Franceschi et al., 2008)

as well. Oligo-Miocene Kargil molasse sediments have yielded palms (e.g., *Sabal*) and temperate *Prunus* (Guleria et al., 1983), indicating a mountainous region nearby (Late Oligocene and Lower Miocene). The Early Miocene plant megafauna of Kasauli Formation predominantly consists of tropical evergreen to moist deciduous species (Srivastava et al., 2014 and references therein). Coastal taxa such as *Acrostichum*, *Garcinia* and *Gluta* indicate a sea near Kasauli (Fig. 3) at the time of deposition of the sediments (Arya and Awasthi, 1995). The Saal tree, *Dipterocarpus* in the Kasaulis is claimed to have arrived from Southeast Asia in the Early Miocene after the final suturing of India and Asia (Shukla et al., 2013; Tiwari et al., 2012). Contrary to this, the pollen record from western India suggests their existence since the Early Eocene (Rust et al., 2010), implying an out of India dispersal instead. Fossil dipterocarps are also known from the late Early Miocene of Kutch and other sites in Gujarat and Rajasthan (Shukla et al., 2013), indicating the presence of wetter conditions with warm and humid tropical rainforests. Interestingly, the Early Miocene of Ethiopia and Uganda has also yielded *Dipterocarpoxydon* and *Dipterocarpus* respectively (Bancroft, 1933; Lemoigne, 1978). Whether these tropical rainforests (Indian and East African) were connected remains to be seen in the Early Miocene fossil record of Arabia and West Asia.

The Middle Miocene Siwalik vegetation predominantly consists of evergreen and some moist deciduous elements (Srivastava et al., 2014). The early Late Miocene landscape was one of tropical forests. These were replaced by subtropical and temperate forests as the gradient increased, and the climate became cooler and drier, indicated by the presence of high altitude taxa *Abies*, *Larix* and *Picea* (Hoorn et al., 2000). A gradual increase in open conditions with landscape dominated by grasslands is accompanied by an increase in shrubs and small trees (Melastoradimataceae/Combretaceae).

Phadtare et al. (1994) found grassland conditions to prevail between ~3.5 and 2.7 Ma, followed by widespread ponding near Dehradun, India. By the Early Pleistocene Siwalik landscape was dominated by wet grasslands interspersed with gallery forests and ponds/swamps. While the Northwest was changing into grassland under a drier regime, the Northeast (Arunachal Pradesh) region still had warm and humid conditions and tropical evergreen rainforest in place (Khan et al., 2011).

Overall the vegetation reflects the tectonic and climate history of the region. The Indian plate, while passing through the tropics in the Eocene and Oligocene, acquired wetlands and rainforests. The temperate mixed with tropical evergreen flora in the Early Miocene deposits indicates uplift of some part of the terrain. The Coastal flora in these deposits suggests the presence of Tethys remnants nearby. The Middle Miocene evergreen to deciduous forests reflect warm and humid conditions and high rainfall in the region. The Late Miocene shrinking of forests and expansion of grasslands may reflect further uplift of the terrain, cooler and drier conditions and monsoon intensification. The Plio-Pleistocene mixed flora, dominated by grasses, pteridophytes and gymnosperms, suggests fluctuating wet/dry and warm/cool conditions.

5. A brief account of the mammal localities/formations and their age

In the Zinda Pir area and Bugti Hills of Sulaiman Province of Pakistan (Fig. 1) the Earliest Miocene (~23–~19 Ma) mammal bearing deposits belong to the upper member of the Chitarwata Formation (Antoine et al., 2013, Table 16.1; Lindsay et al., 2005). The Kargil Molasse in India has yielded the artiodactyl *Sivameryx* and the rodent *Democricetodon*, assignable to Early Miocene (Prasad et al., 2005). From the Indian Murrees, Kumar and Kad (2003) reported the Early Miocene cricetid, *Primus microps* from Kalakot (Jammu and Kashmir). *Prodeinotherium* is reported from the Upper Dharamsala beds of Kangra Valley (Tiwari et al., 2006). Flynn et al. (2013) place the lowest Stratigraphic Datum of *Prodeinotherium* at ~23 Ma. In Kutch, western India, mammal and other terrestrial vertebrate remains have been preserved on a marine fossiliferous surface, biochronologically dated to 16.5 ± .5 Ma (Bhandari et al., 2010, Table 1). Several genera of the Chitarwata Formation continue into the Vihowa Formation (~19–~11 Ma) in Pakistan (Antoine et al., 2013, Table 16.2). In the Potwar Plateau of Pakistan lower Siwalik deposits (Kamlial Formation, ~18–14 Ma) have yielded a diverse assemblage (Barry et al., 2002, Colbert, 1935; Raza, 1997).

The Middle Miocene Chinji Formation in the Potwar ranges from 14.2 to 11.2 Ma (Barry et al., 2002) and its diverse fauna includes the ape *Sivapithecus* (Colbert, 1935; Raza, 1997). In the Indian part the typical Chinji lithology of the red beds produces the primate locality of Ramnagar. The mammalian fauna represents ~14 to 12 Ma based on rodent biochronology (Sehgal and Patnaik, 2012). In the Northeast of India (Garo Hills, Assam) *Microbunodon silistrensis* has been recorded from marine sequences suggesting an age of late Early Miocene (17.8 Ma) to Middle Miocene (11.4 Ma) (Lihoreau et al., 2004). Just across the border *Microbunodon silistrensis* occurs in the Pegu beds of Myanmar (Takai et al., 2006).

The Late Miocene Nagri Formation (11.2 to 9 Ma) in the Potwar has yielded several taxa that were already present in Chinji. The African aardvark *Orycteropus* appears for the first time in the Siwaliks at 13.6 Ma (Barry et al., 2002). The Dhok Pathan Formation (10.1 to 3.5 Ma) in Pakistan yields diverse mammalian taxa that appear for the first time (Barry et al., 2002; Colbert, 1935; Raza, 1997). The magnetostratigraphically dated Haritalyangar locality (10.1–8.5 Ma) is famous for its similar mammalian wealth including the primates *Indopithecus*, *Sivapithecus*, *Indraloris*, *Sivaladapis* and *Pliopithecus* (Patnaik, 2013; Pillans et al., 2005 and references therein). The Kalagarh mammal locality in Uttarakhand, India is like Haritalyangar, with a similar range (9.3 and 8 Ma) (Patnaik, 2013). The Baripada Beds exposed in the Mayurbhanj District of Orissa, India have yielded *Tetraconodon* cf. *intermedius* that ranges from 10–8 Ma (Sharma and Patnaik, 2013). The Late Miocene (10.1–9.7 Ma) mammalian assemblage from Nurpur (Himachal Pradesh, India) is also similar to that of Haritalyangar (Patnaik, 2013).

Perim Island (Gujarat, India) preserves a diverse assemblage of mammals in a conglomeratic facies (Prasad, 1974). As the deposits contain *Hipparion antelopinum*, they would

be younger than 10.7 Ma (Barry et al., 2002). If the presence of *Selenoportax vexillarius* is confirmed then the deposits would fall between 10.2 and 9.8 Ma (Gentry et al., 2014). The caprine *Nisidorcas* (Bouvrain, 1979) is an important biochronological indicator occurring at several sites in Greece and Turkey between 8.2 and 7.5 Ma (Bonis and Koufos, 1999; Sen et al., 2000). *Nisidorcas planicornis* occurs just at one site in the Siwaliks dated to 9 Ma (Gentry et al., 2014). Therefore, Perim Island deposits could be 10–9 Ma old. Bokabil Formation (Tripura, India) assemblage includes the proboscideans *Gomphotherium angustidens* and *Stegolophodon cautleyi*; the perissodactyl *Hipparion theobaldi*, the artiodactyls *Dorcatherium*, *Pachyportax* sp. and *Propotamochoerus hysudricus* (Trivedy, 1980). The presence of *Hipparion* would make the deposits younger than 10.7 Ma and *Propotamochoerus hysudricus* further constrains these deposits between 10.2 and 6.8 Ma (Barry et al., 2002). The fauna shows very close affinity to those found in Myanmar.

The Pliocene Tatrot Formation in Pakistan represents 200,000 years from 3.5 to 3.3 Ma (Barry et al., 2002) and has yielded *Anancus*, *Hippohyus*, *Hippotragus* and *Hydaspicobus* (Colbert, 1935; Pilgrim, 1939). The Lower Pliocene record from Saketi and Upper Pliocene sediments in the Jammu region have yielded several mammals ranging in age between ~4.5 and ~2.5 Ma (Nanda, 2013; Patnaik, 2013).

The Pleistocene Pinjor Formation, India (2.58–2.2 Ma) exposed around Chandigarh and Pabbi Hills, Pakistan has yielded a diverse mammal assemblage (Dennell et al., 2006; Nanda, 2013; Patnaik, 2013).

The Himalayan inter-montane basin in the Kashmir Valley called Karewas has yielded diverse mammals (Kotliya, 1990). Except for the additions of murid *Rhagapodemus*, microtine *Kilarcola* and shrew *Episorculus*, the presence of Siwalik Plio-Pleistocene elements in the Karewas indicates similar ecological and climatological conditions. Valdiya (1993) suggested that the Pir Panjal rose by 2700–3000 m since the Middle Pleistocene.

In the peninsula, Attirampakkam site (Tamil Nadu, India) has been dated to >1 Ma (Pappu et al., 2011) and has yielded *Bubalus/Bos*, *Boselaphas* and *Equus* (Chauhan, 2008). Bhagalpur site in Ganga plain has yielded a diverse assemblage that led Verma et al. (1998) to propose an Early Pleistocene age 1.5–1 Ma. As one of the richest sites in the Peninsula and the only to have produced remains of archaic *Homo sapiens*, the Narmada Valley sediments have yielded a diverse fauna (Chauhan, 2008 for a review). Patnaik et al. (2009) provided a time frame for the lower unit belonging to the Surajkund Formation ranging from at least ~50 Ka to ~160 Ka and suggested extensive reworking of the fossils. Dutta (1976) reported *Panthera cf. leo* (lion) and *Crocuta cf. sivalensis* (spotted hyena) from West Bengal, India. The age of these deposits is not certain but the co-occurrence of microlithics places them in the Late Pleistocene. The Indogangetic region has several sites with mammals (Son, Belan, Paimar, Kalpi etc. Badam, 2013). Godavari and Krishna Valleys have yielded fauna similar to that of the Narmada Valley (Chauhan, 2008).

The Kurnool Caves in South India have yielded the most diverse Late Pleistocene fauna (Prasad, 1996). Roberts et al. (2014) found 20 mammalian taxa continue to exist over the

last 200 Ka, except for the African immigrant *Theropithecus cf. gelada* at ~100 Ka. The Ratnapura fauna (Late Pleistocene) of Sri Lanka includes elephants, hippos, rhinos, a primate, carnivores and artiodactyls (Deraniyagala, 1992).

6. Data Analyses and Discussion

The present paper attempts to evaluate the published temporal distribution of Neogene and Quaternary mammal genera (mostly terrestrial) of the Indian subcontinent at 1 m.y. intervals. Fig. 2 summarizes the first and last appearances of creodonts, carnivores, proboscideans, artiodactyls, perissodactyls, primates and rodents. Based on Fig. 2, bivariate plots show the number of first and last appearances, immigrants and overall diversity of these mammalian genera (Fig. 4C).

6.1. Distribution and Dispersal of mammals

The Laurasiatheres, which include artiodactyls, perissodactyls, bats, carnivores and pangolins (O'Leary et al., 2013) were present in Eurasia, India and North America in the Early Eocene (~55 Ma, Rose, 2006). New finds suggest that perissodactyls were present on the Indian plate in the Early Eocene (Rose et al., 2014) prior to its collision with Asia. The timing of India-Asia collision was mostly complete by ~50 Ma but, a recent study (Hinsbergen van et al., 2012) suggests that the “hard” collision of the Indian plate happened between 25 and 20 Ma. This “hard” collision most likely led to the formation of the oriental biogeographic province, and until the Early Miocene the Himalayas possibly were not high enough to hinder dispersal of early artiodactyls and perissodactyls within this province and beyond.

Afrotheres (proboscideans, hyracoids, embrithopods) dominated Africa, as indicated by the Late Oligocene (27 Ma) Chilga assemblage of Ethiopia (Kappelman et al., 2003). Around the Oligo-Miocene boundary ~23 Ma a rotatory tectonic movement of the Afro-Arabian plate resulted in a land connection between Afro-Arabia and Eurasia, allowing dispersal (Bernor et al., 1987) (Fig. 3). This connection is also known as the “Gomphotherium Land Bridge” (Rögl, 1999; Tassy, 1990). After a polar ice increase around this time and an overall cooler climate and a drop in sea level, the subsequent closure of the Tethys led to a reorganization of ocean currents and a change in climate toward an increase in temperature and the Middle Miocene Climate Optima (Miller et al., 2005; Zachos et al., 2001) (Fig. 4A). In the Early Miocene (~23–~16 Ma), the Indian subcontinent broadly experienced warm and humid conditions, and tropical evergreen forests covered a large part of the subcontinent. The dipterocarps extended from Myanmar in the east to Kutch and Kasauli in the west, and are also known from Ethiopia and Mount Elgon, Uganda (Bancroft, 1933; Lemoigne, 1978). The other taxa that are common between Mount Elgon and Kasauli Formation are *Bauhinia*, *Cassia* and *Dalbergia* (Srivastava et al., 2014 and references therein). Overall Early Miocene African sites show evidence of a mosaic of forests (rainforests, deciduous, evergreen) (Jacobs et al., 2010; Retallack, 1991), but at some sites there is evidence of open/grassland conditions as well

(Ungar et al., 2012). The presence of similar vegetation types between Africa and the Indian subcontinent might have facilitated the dispersal of browsing mammals between them (Fig. 3; 4B).

6.1.1. Early Miocene (23–16 Ma)

Prodeinotherium and *Gomphotherium* are considered to be among the first African genera to cross the Afro-Arabia-Eurasia land bridge (Fig. 3) and reach the Indian subcontinent Laki Hills in Sindh and Bugti Hills in Baluchistan and also Lesbos Island, Greece and further west (Antoine and Welcomme, 2000; Koufos et al., 2003; Rögl, 1999; Tassy, 1990; Tiwari et al., 2006). The Lowest Stratigraphic Datum of *Prodeinotherium* is now at ~23 Ma (Flynn et al., 2013) and *Gomphotherium* now occurs ~22 Ma, implying a much earlier migration event of these two genera (Antoine et al., 2013 and references therein). The excellent swimming ability of proboscideans may explain their early dispersal out of Africa before the establishment of the Afro-Eurasian land bridge. *Eumyarion* had an earlier (~22.8 Ma) occurrence in China (Fortelius, 2013, NOW database) so similar rhizomyines of Pakistan appear to be an early immigrant to the subcontinent. The same can be said about *Spanocricetodon*, *Democricetodon* and *Primus* (Flynn and Wessels, 2013; Wessels, 2009) (Fig. 4B).

In the opposite direction a major dispersal of Eurasian mammals took place (e.g., rhinos, chalicotheres and suids) into Africa between 20 and 18 Ma (Bernor et al., 1987; Bishop, 2010; Coombs and Cote, 2010). Sanitheres from Bugti indicate their origin in the subcontinent and dispersal to Africa (Orliac et al., 2010). *Dorcatherium* is another genus that indicates an Early Miocene faunal exchange because it occurs almost simultaneously at 22 Ma in Kenya (Pickford, 2001) and in the Chitarwata Formation of Pakistan (Antoine et al., 2013; Lindsay et al., 2005).

The creodonts dispersed from Africa to Asia whereas the carnivores moved from Asia to Africa (Barry, 1988). The Bear-Dog, *Amphicyon* is recorded from the Earliest Miocene sediments of Bugti Hills (Antoine et al., 2013) and most likely reached Africa via the Gomphotherium Land Bridge.

Zygodolophodon appears at ~20 Ma, followed by *Choerolophodon* and cf. *Protoanancus* in the subcontinent. *Pterodon* also appears around this time from Africa. Squirrels (cf. *Tamiops*, cf. *Orienscivrus*), *Megacricetodon*, *Myocricetodon*, *Diatomys* and *Marymus* were most likely immigrants from the east (Flynn and Wessels, 2013). Between 19 and 18 Ma, the African creodont *Hyainailouros* and the thryonomyid *Kochalia* appeared in the subcontinent, while *Tamiops*, *Orienscivrus*, and *Sayimys* were most likely immigrants from the east. Around 18.5 Ma a murid close to *Potwarmus* and the ctenodactylid *Sayimys* dispersed to Saudi Arabia and North Africa (Flynn and Wessels, 2013 and references therein). The rhizomyine *Prokanisamys* also spread to Saudi Arabia and North Africa in the Early Miocene.

Gomphotherium and *Zygodolophodon* dispersed to Europe at around 18 Ma. *Gomphotherium* is known from China at ~18 Ma (Fortelius, 2013, NOW database). The anthracothere *Sivameryx* entered Africa in the Early Miocene, as it is known from Kenya at around 18–17.5 Ma, and Libya and Egypt at around 17–16.5 Ma (Pickford, 1987) (Fig. 4).

Around 18 Ma, the thryonomyid *Kochalia* reached Pakistan from Africa (Wessels, 2009).

Between 17 and 16 Ma, *Deinotherium*, *Dissopsalis* and *Dionysopithecus* emigrated from Africa and *Aliveria*, *Funambulus*, *Punjabemys*, *Mellalomys*, *Potwarmus* and *Kanisamys* were most likely North and East Asian additions to the subcontinent (Flynn and Wessels, 2013). The creodont *Dissopsalis* appears in the Siwaliks at 16.1 Ma (Barry, 1988). Then, *Deinotherium* reached Europe and *Zygodolophodon*, and *Choerolophodon* reached China ~16.5 Ma (van der Made, 2010) and van der Made (2010) suggests that by then *Choerolophodon* had evolved in South Asia from *Gomphotherium* spreading to Africa. At this time another Eurasian dispersal into Africa involved the bovid *Eotragus* and suid *Listriodon* (Bishop, 2010; Gentry, 2010; Pickford, 1981). The Kutch suid *Libycochoerus fategadensis* is close to the African species *Libycochoerus anchidens* (van der Made, 1996) and is another taxon that indicates faunal exchange around this time (Bhandari et al., 2010). *Dionysopithecus* is an early immigrant from Africa known from ~16.5 Ma Manchar sediments of Pakistan (Bernor et al., 1988).

6.1.2. Middle Miocene (16–11.5 Ma)

Before 16 Ma, African apes were most likely forest-dependent (Andrews and Kelley, 2007). At the beginning of the Middle Miocene, seasonal forests and woodlands expanded both in Africa and Eurasia. The early apes probably adapted to these more open conditions and dispersed to Turkey and Europe just before the Langhian transgression (Andrews and Kelley, 2007). Apes ancestral to the Siwalik Miocene ape *Sivapithecus* may have arrived in the Indian subcontinent from the west (Turkey) sometime around 15–16 Ma (Begun, 2005).

Between 15 and 14 Ma, the bovids *Sivaceros*, *Sivoreas*, *Elachistocerus* and *Kubanotragus*, and the rodents *Atlantoxerus*, *Callosciurus*, *Heteroxerus*, *Sciurotamias*, *Eutamias*, *Dremomys*, *Dakkamys*, *Antemus*, and *Myomimus* appeared in the Indian subcontinent (Fig. 2). The bovids most likely had their ancestry in Eurasia and that of the sciurids perhaps in Asia (Flynn and Wessels, 2013). Around this time *Stegolophodon*, having evolved in North Asia from *Gomphotherium*, dispersed southward, whereas *Paratralophodon* may be endemic (van der Made, 2010). Likely immigrants from East Asia around 14–13 Ma are the suids *Conohyus* and *Hyotherium*, and the bovids *Hypsodontus*, *Helicopotax*, and *Gazella*. The thryonomyid *Paraulacodus* arrived in the subcontinent at 13 Ma from Africa (Flynn and Winkler, 1994). The otter *Vishnuonyx* occurs in Africa and the Indian subcontinent almost simultaneously at ~12 Ma (Pickford, 2007). The Eurasian bovid *Tethytragus* and Asian hystricid *Sivacanthion* also appeared around this time. Between 12 and 11 Ma Asian suids *Tetraconodon* and *Hippopotamodon*, and the Eurasian suid *Schizochoerus*, and the bovid *Protoryx* seem to be immigrants as they are known in older deposits in Asia and Eurasia respectively (NOW database, Fortelius, 2013).

6.1.3. Late Miocene (11.6–5.3 Ma)

By the Late Miocene monsoons intensified and grasslands dominated the landscape at the expense of forests.

The equid *Hipparion* immigrated from North America, arriving in China and Europe somewhat before 11 Ma (MacFadden, 1992). *Hipparion* appeared for the first time in the Siwaliks at 10.7 Ma (Barry et al., 2002). *Progonomys* dispersed to the west, appearing in North Africa after 12 Ma (Winkler, 1994), and Europe and China by 10 Ma (Kappelman et al., 2003; Qiu et al., 2013). *Karnimata* and cf. *Parapelomys* are also known to occur in 9–10 Ma old sediments of Namibia and East Africa (Conroy et al., 1992; Senut et al., 1992).

Kobus porrecticornis, according to Gentry et al. (2014), ranges in Pakistan from 8.1 to 7.7 Ma. *Kobus porrecticornis* has been recorded from East and South Africa between 6.5 to 5 Ma, indicating intercontinental dispersal and similar ecological conditions during the Latest Miocene (Bibi, 2011). Another Siwalik bovid *Prostrepsiceros vinayaki* ranging from 9.3–7.9 Ma, occurs in Arabia around 8–6 Ma and in Africa between 5.7 and 5.4 Ma (Bibi, 2011). At ~6.3 Ma the colobine monkey *Presbytis* appears in the Siwalik record from Europe or Africa (Barry, 1987). *Propotamochoerus hysudricus* is an immigrant at ~10 Ma (Flynn et al., 2014), most likely from China where the genus occurs in older deposits. Later it spreads westward to Abu Dhabi (Bishop, 2010).

Another important event is the immigration of leporids in the Late Miocene. They disperse to south Asia via China from North America around 7.4 Ma in the form of *Alilepus* which in turn disperses into Africa around 7 Ma (Flynn et al., 2013). *Hystrix* appears for the first time at 8 Ma, arriving most likely from the east (Flynn and Wessels, 2013). At around 8 to 9 Ma *Abudhabia* came from the east and *Parapodemus* arrived from the west (Flynn and Wessels, 2013; Fortelius, 2013 NOW database). The luterine *Sivaonyx*, widespread in India, Pakistan, China, Thailand, Turkey and Germany during the Middle to Late Miocene, most likely dispersed to Africa in the Late Miocene (Grohé et al., 2013).

6.1.4. Early Pliocene (5.3–3.6 Ma)

The Early Pliocene was warm and humid, and the landscape was dominated by wooded grasslands. *Mus* appears to be an immigrant to the Indian subcontinent ~7 Ma (Flynn et al., 2014) and is known from Early Pliocene (4.5 Ma) deposits of Kenya, Africa (Patnaik, 2014; Winkler, 2002). *Golunda* group murids are known from Early Pliocene of Morocco and Ethiopia (Fortelius, 2013 NOW database). *Hexaprotodon sivalensis* and *Elephas planifrons* are immigrants from Africa to the Siwaliks in the Late Miocene (~6 Ma) and Late Pliocene, respectively (Barry et al., 2002; van der Made, 2010), although Barry et al. (2002) suggest an earlier (5.9 Ma) FAD for *Elephas planifrons* in the Siwaliks. *Anancus*, most likely evolving from *Paratetralophodon* in the subcontinent, disperses to Africa, Europe and North Asia in the Late Miocene (van der Made, 2010). At around 6 Ma, Asian *Paracamelus* arrived from North America and evolved into *Camelus* (van der Made, 2010), later dispersing to the subcontinent in the Late Pliocene. *Stegodon* may have originated in S. Asia from *Gomphotherium* in the Early Pliocene (van der Made, 2010).

6.1.5. Late Pliocene (3.6–2.6 Ma)

The Late Pliocene saw cooler and drier conditions. The African bovid *Hippotragus* dispersed to the subcontinent in the Late Pliocene (Vrba and Gatesy, 1994). The presence of palaeartic elements *Rhagapodemus* and *Kilarcola* in the Karewas of Kashmir may indicate a shift of the Palaeartic province southward during the Late Pliocene cooling. *Rhagapodemus* is an immigrant from Europe (Kotliia, 2013). The deer *Cervus* was also an immigrant from Europe (Barry and Flynn, 1989).

6.1.6. Early Pleistocene (2.6–780 Ma)

A major faunal turnover is indicated at the N/Q boundary (Patnaik, 2013 and references therein). The African bovids, *Oryx*, *Damalops*, *Vishnukobus*, *Sivacobus* and the hyaenids *Crocota* and *Pachycrocota* appear in the Pinjors (Dennell et al., 2006; Vrba and Gatesy, 1994). *Elephas planifrons* is replaced by another African immigrant *Elephas hysudricus* at around 2.7 Ma (van der Made, 2010). *Theropithecus* and *Elephas* are immigrants, originally from Africa, whereas the saber tooth *Megantereon* and the giant hyena *Pachycrocota* most likely came via Europe (Palmqvist et al., 2007). *Equus* and *Camelus* entered the subcontinent at this time from the west. *Tatera*-like gerbils are known from older deposits in Ethiopia (5.7 Ma) and Kenya (4.17 Ma) (Fortelius, 2013 NOW database) and arrived in the subcontinent at ~2 Ma. During the Early Pleistocene, Indian subcontinent taxa were widespread throughout North Africa, Saudi Arabia, Middle East, Myanmar and China. Common elements at Ain Hanech (Algeria) include *Equus* and *Gazella*; from Ubeidiya (Israel) are *Ursus*, *Canis*, *Panthera*, *Megantereon*, *Crocota*, *Lutra*, *Equus*, *Sus*, *Camelus*, *Bos*, *Gazella* (Tchernov, 1987); from Dmanisi (Georgia) are *Ursus*, *Canis*, *Panthera*, *Megantereon*, *Pachycrocota*, *Equus*, *Cervus* and *Gazella* (Gabunia, 2000). Nafud (Saudi Arabia) records *Crocota*, *Oryx*, *Panthera*, *Elephas*, *Equus* and *Hexaprotodon* (Dennell, 2003). Central Asian Latest Pliocene (1.77–1.95 Ma) taxa include *Canis*, *Ursus*, *Megantereon*, *Equus*, *Sivatherium* and *Damalops* (Sotnikova et al., 1997). The Indian genus *Hemibos* occurs in the Early-Middle Pleistocene transition in Italy (Martínez-Navarro and Palombo, 2004). Recently *Elephas hysudricus* has been recorded from Middle Pleistocene of Levant (Lister et al., 2013). *Elephas (Paleoloxodon) namadicus* arrived from Africa around 1 Ma (van der Made, 2010). Takai et al. (2006) provide a list of Early Pleistocene Upper Irrawaddy fauna of Myanmar held in common with Pinjor such as *Merycopotamus dissimilis*, *Potamochoerus*, *Hexaprotodon*, *Cervus*, *Hemibos*, *Rhinoceros*, *Stegodon* and *Elephas*. However, the Upper Pliocene rodent fauna from Myanmar is endemic and does not share any common elements with the Indian subcontinent (Nishioka et al., 2015). Common elements between the Early Pleistocene of China and India are *Megantereon*, *Panthera*, *Pachycrocota*, *Crocota*, *Canis*, *Equus*, *Rhinoceros*, *Stegodon*, *Gazella*, *Leptobos*, *Hemibos*, *Potamochoerus* and *Sus* (Qiu et al., 2013). *Procyonocephalus*, known from Pinjor, occurs at the Early Pleistocene (1.2 Ma) Sanhe site of China. Java shares several mammals with the subcontinent and sometime around 1 Ma (Ci Saat site), *Hexaprotodon*, *Axis*, cervid, *Panthera*, *Stegodon* and most

probably *Homo erectus* entered Java (van den Bergh et al., 2001).

6.1.7. Middle Pleistocene (.780–.120 Ma)

A drop in sea level and the presence of wooded grassland (Kedung Brubus site, Java) possibly facilitated dispersal of mammals, such as *Elephas hysudrindicus* (via Myanmar), *Cuon*, *Panthera*, *Hexaprotodon*, *Muntiacus*, *Rhinoceros*, *Sus* through the Siva-Malayan route, the ancient hypothetical route connecting Siwaliks and the Malayan region. The forest dweller *Atherurus karnulensis* is known from the Middle to Late Pleistocene of South China and Vietnam (van der Weers, 2002) and may suggest some biogeographic connection. The rodent *Bandicota* is known from Middle Pleistocene Liujang Cave of China and the Thum Wanim Nakih site of Thailand (Fortelius, 2013 NOW database).

6.1.8. Late Pleistocene (.120–0.010 Ma)

In the Late Pleistocene large mammals are found widely across the Peninsula (Fig. 1) and a diverse assemblage comes from the Kurnool Caves. The Latest Pleistocene climate became arid causing extinction of *Stegodon*, *Hexaprotodon* and confinement of *Rhinoceros* to the north and the north-east. There is no evidence of any major dispersal out of or into the subcontinent in the Late Pleistocene. However, *Theropithecus cf. gelada* from Kurnool Cave (Roberts et al., 2014) may suggest an immigration of this African element. The date of arrival of *Homo sapiens* from Africa is highly debated, but its presence in the subcontinent by 50 Ka is accepted widely.

6.2. An assessment of turnover pulses

Most of the faunal turnovers (immigration, first and last appearances) took place at the times of major tectonic episodes, sea level drops, climate and vegetation changes at 23–22, 20–18, 17–16, 15–14, 11–10, 9–8, 3–2 and 1–0 Ma. The overall combined and separate generic diversity of various mammal families discussed here also varied around these times (Fig. 5). Between 23 and 22 Ma, the sudden appearance of several genera mostly of Asian origin might support dispersal from north and east. Between 20 and 19 Ma, the Afro-Arabian and Eurasian Land bridge was in place, there was a major drop in sea level, and the presence of rainforests in Eastern Africa and the subcontinent most probably facilitated a major faunal exchange between Eurasia and Africa, and the increased first appearances of sciurid rodents, rhinocerotids, proboscideans and anthracotheres (Fig. 4 B, C & D). A peak in the number of last appearances followed (19–18 Ma). Between 17 and 16 Ma, a major Himalayan uplift, a drop in the sea level and warm and humid conditions most probably led to a rise in the number of first appearances and immigrants, mainly sciurids and rhinocerotids; 15–14 Ma saw a major influx of immigrants, first appearances and a rise in murid, proboscidean and anthracothere diversity probably influenced by a drop in the sea level and the Middle Miocene Climate Optima. Between 10 and 11 Ma, coinciding with a sea level drop and monsoon intensification, a moderate rise in the number of first and last appearances and immigrants is observed. The diversity of sciurids, rhinocerotids, equids,

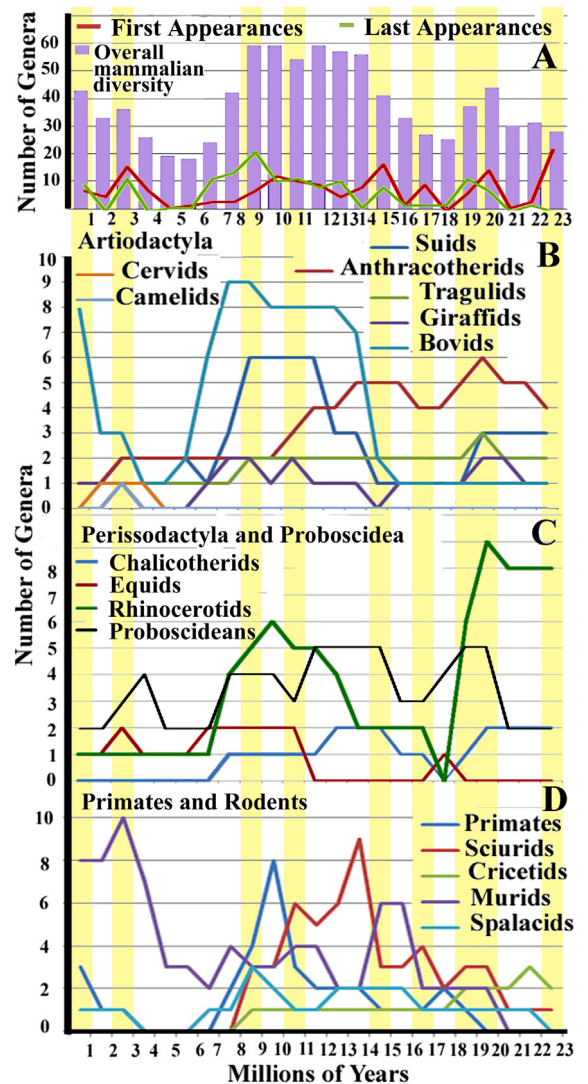


Fig. 5. Neogene–Quaternary Mammalian diversity at the genus level. A: Combined mammalian diversity and number of first and last appearances. B: Diversity of artiodactyls. C: Diversity of perissodactyls and proboscideans. D: Rodent and primate diversity. Yellow vertical bands correspond to major turnover pulses.

Fig. 5. Diversité mammalienne Néogène–Quaternaire au niveau du genre. A : Combinaison de la diversité mammalienne et du nombre des premières et dernières apparitions. B : Diversité des artiodactyles. C : Diversité des périssoactyles et des proboscidiens. D : Diversité des rongeurs et des primates. Les bandes verticales jaunes correspondent aux principales impulsions de *turnover*.

suids and bovids is quite high during this time (Fig. 5). The Late Miocene monsoon intensification and a major vegetation change (Cerling et al., 1997; Harrison et al., 1993) most probably led to a steep rise in the number of last appearances between 9 and 8 Ma. A Major Himalayan uplift, monsoon intensification, drier conditions and a drop in sea level possibly led to a steep rise in the number of first and last appearances, immigrants and murid diversity between 3 and 2 Ma. Finally, a drop in sea level and wooded grassland at ~0.8 Ma might have facilitated a rise in number of first and last appearances, immigrants and

bovid diversity. Periods of endemism and immigration fluctuated but persisted throughout the Miocene (Flynn et al., 2014).

7. Concluding Remarks

Although the Indian Subcontinent appears like a fortress today, surrounded by the Himalayas in the north, north-west, north-east, the Thar Desert in the west and the Indian Ocean in the south, it has never really remained inaccessible for long periods to dispersing Neogene and Quaternary mammals. However, due to constantly changing tectonic, climatic and vegetation scenarios of the subcontinent, the faunal composition changed continuously, leading to immigrations, emigrations, extirpations, and endemic evolution. The subsiding foreland basins along the Himalayan foothills helped to preserve a long record of sediments and fauna, whereas in the Peninsular region the Miocene mammals of Kutch, Perim Island and Baripada Beds were preserved due to marine regressions and transgressions.

A strong correlation of tectonic, climate, sea level and vegetation changes with turnover pulses of mammalian genera occurred around 23–22, 20–18, 15–14, 11–10, 9–8, 3–2, and 1–0 Ma in the Indian subcontinent. Dispersals along the coast from the west into the subcontinent may explain the occurrence of immigrant mammals at older sites in the ancient coastal areas such as Chitarwata, Kargil and Kutch in the Early Miocene. The main migrations into the subcontinent were from the west (Africa, West Asia and Europe) throughout the Neogene and Quaternary, whereas those from the east (Myanmar, Thailand and South China) were few, limited mostly to small mammals during the Miocene (Fig. 2). The Early Pleistocene saw the dispersal of several mammals from the west and towards Java in the east via Myanmar, and most likely included *Homo erectus*.

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