

*Review Article*

## Neogene Climate, Terrestrial Mammals and Flora of the Indian Subcontinent

RAJEEV PATNAIK<sup>1,\*</sup> and VANDANA PRASAD<sup>2</sup>

<sup>1</sup>Center for Advanced Study in Geology, Panjab University, Chandigarh, India

<sup>2</sup>Birbal Sahni Institute of Palaeosciences, Lucknow, India

(Received on 10 April 2016; Accepted on 28 April 2016)

The present review compiles the work done in and around India during 2011-2015 on the terrestrial climate, fauna and vegetation changes during the Neogene. Tectonics that led to the final closure of Tethys, uplift of the Tibetan plateau, land connection between Africa and Eurasia played a major role in the climatic variability and paleobiogeographic history of fauna and flora of the Indian subcontinent. Though the timing of initiation of monsoon is still a debatable issue, establishment of seasonal reversal in wind direction pattern during summer and winter period and development of monsoonal climate in larger parts of the Indian subcontinent is characteristic of Neogene. Fossil records of flora and fauna provide evidence of warm and humid climate of early Neogene, which then shifted to cooler and drier conditions during the late Neogene. This shift in the climatic conditions resulted in a major vegetation change in the Indian subcontinent with Early and Middle Miocene being dominated by C<sub>3</sub> vegetation, and warm and humid tropical flora in low land areas while Late Miocene and Pliocene saw the dominance of C<sub>4</sub> grasslands. Influenced by this major vegetation and ecological shift around Late Miocene, several browsing mammals of the Early and Middle Miocene landscape gave way to mostly grazing mammals of the Late Miocene and Pliocene time.

**Key words:** Indian Subcontinent; Neogene; Mammalia; Vegetation; Dispersal; Paleobiogeography

### Introduction

Being part of the Oriental Biogeographic Province the fauna and flora of India have evolved under an essentially monsoonal climatic condition during much of the Neogene. The Neogene climate was influenced by several factors that include suturing of the Indian and Asian plates, uplift of the Himalayas, change in the ocean current directions and northern hemisphere glaciations. Overall, the Early Neogene witnessed a warm and humid condition followed by a rather cooler and drier regime during the later stages.

The present review compiles the work done in the Indian subcontinent in the last five years on Neogene terrestrial fauna and flora and their relation to the overall Neogene climate change. The Neogene faunal sites of India are primarily located in the Siwalik fluvial deposits that stretches from Pakistan in the west to Assam in the North East exposed all along

the Himalayan foothills (Fig. 1). However, Early Miocene fossils are also known from the Trans-Himalayan Kargil Molasse Group and foreland basin Murree Formation and its equivalents the Dharamsala, Dagshai and Kasauli Formations. In the peninsular India, Middle and Late Miocene mammals are known from the Kutch basin (Bhandari *et al.*, 2015). In the North East of India, Garo Hills represent a Middle Miocene Locality (Patnaik, 2016 and references therein). The localities in the peninsula that can be assigned a Late Miocene age are Perim Islands (Patnaik, 2016 for a review) in the west and Baripada Beds (Sharma and Patnaik, 2013) and Tripura in the east.

### Early Miocene (~23 to ~16 Ma) Fauna and Vegetation

Early Neogene fluvio-deltaic sediments are exposed in Trans Himalayas (ex. Kargil deposits), Himalayan

\*Author for Correspondence: E-mail: rajeevpatnaik@gmail.com



Fig. 1: Map of India and neighbouring countries showing the distribution of terrestrial Neogene deposits

foreland basin (ex. Murrees) and Sulaiman Province of Pakistan. In the Bugti and Zinda Pir Dome areas of Pakistan these fluvio-deltaic deposits have yielded a wide variety of fossil mammals (Antoine *et al.*, 2013). From the Kargil deposits Late Oligocene to Early Miocene rodents and ungulates similar to those occurring in the Bugti and Zinda Pir areas are found (Prasad *et al.*, 2005; Patnaik, 2016 for a review).

The foreland deposits referred to as the Murree Group are best recorded from the Murree Hills of Pakistan and Jammu and Kashmir region in India. Their equivalent in Kangra, Himachal Pradesh, are referred to as the Dharamsala Group, and in the Simla region as the Dagshai (lower sequence) and Kasauli Formations.

Kargil Molasse have yielded the artiodactyl and the rodent *Democricetodon* assignable to early

Miocene following the occurrence of the anthracothere *Sivameryx* at Bugti and Zinda Pir Hills, from ~22 to ~18 Ma (Antoine *et al.*, 2013) and at Potwar from 17.8 to 15.6 Ma (Barry *et al.*, 2013).

Kargil molasse deposits have yielded remains of palms *Sabal*, *Tachycarpus*, *Amesoneuron* and *Palmacites*. Guleria *et al.* (1983) reported *Prunus* from the Liyan Formation (equivalent to Kargil Molasse). The early Miocene plant mega fossils of Kasauli Formation predominantly consists of tropical evergreen to moist deciduous species that include *Ficus*, *Chukrasia*, *Garcinia*, *Gluta*, *Kayea*, *Mallotus*, *Mesua*, *Persea* and *Phyllanthus* (Srivastava *et al.*, 2014 and reference therein). *Dipterocarpus* fossil wood in the Kasaulis, as well as fossil fruits from Early Miocene sediments of Kutch, Gujarat, comparable to *Shorea macroptera* Dyer of the Malayan Peninsula (Shukla *et al.*, 2012), suggest

that the family Dipterocarpaceae might have arrived from the southeast Asia in the early Miocene (Tiwari *et al.*, 2012). Contrary to this, the pollen record from western India indicates its existence since the Early Eocene (Dutta *et al.*, 2011; Rust *et al.*, 2010). The Kasauli Formation has also yielded algal, fungal and pteridophytic spores, gymnospermous and angiospermous pollen indicating presence of a moist subtropical climate with some montane elements (Rao and Verma, 2014 and reference therein). Fossils of Dipterocarpaceae are known from late Early/Middle Miocene of Kutch and other sites in Gujarat and Rajasthan (Shukla *et al.*, 2012). In another study, two fossil woods, namely *Bauhinium palaeomalabaricum* (Fabaceae) and *Ebenoxylon indicum* (Ebenaceae), described from early Miocene of Kutch suggest a warm and humid climate with good rainfall during early Miocene in the region (Shukla *et al.*, 2015).

The Murree/Dharamsala Group, of Himalayan foreland basin contain *Deinotherium* sp. *Teleoceras* (*Brachypotherium*) *fatehjangense*, *Palaeochoerus* sp. (*Conohyus*) and *Microbunodon* sp. and *Gonotelma* sp. and can be correlated well with early Miocene of Upper Chitarwata Formation and lowest Vihowa Formation in the Bugti Hills (Welcomme *et al.*, 2001; Antoine *et al.*, 2010; 2013). Kumar and Kad (2003) reported a cricetid, *Primus microps* from Kalakot (Jammu and Kashmir) and opined that the Murree sediments of India are of Early Miocene age. *Prodeinotherium* from the Upper Dharamsala beds of Kangra Valley may also indicate Early Miocene age (Tiwari *et al.*, 2006; Flynn *et al.*, 2013).

The diverse faunal assemblage from Kutch, Gujarat includes *Deinotherium sindiense*, *Gomphotherium* indet., *Brachypotherium* sp., *Parabrachyodus hyopotamoides*, *Sivameryx palaeindicus*, *Conohyus sindiensis*/*Tetraconodon malensis*, *Libycochoerus fategadensis*, *Giraffokeryx punjabiensis* and *Dorcatherium minus* (Bhandari *et al.* 2010; Patnaik *et al.*, 2014). The age of the mammal fauna from Tapar and Pasuda sections of Kutch, described previously by Bhandari *et al.* (2010), has now been revised to basal Late Miocene (~11-10 Ma) based on the presence of *Hipparion* (Bhandari *et al.* 2015). Bhandari *et al.* (2015) also discovered a maxilla of a chimpanzee-sized sivapithecine hominoid from these deposits making it

the first such find from peninsular India. A new fossil suid *Kachchhchoerus salinus* has also been described by these authors.

### Middle Miocene (~16 to ~11.5 Ma) Fauna and Vegetation

The Middle Miocene Siwalik vegetation predominantly consists of evergreen and some moist deciduous elements (Srivastava *et al.*, 2014). The evergreen elements include *Bouea*, *Bursera*, *Calophyllum*, *Dipterocarpus*, *Garcinia*, *Hopea*, *Kayea*, *Polyalthia*, *Saccopetalum tomentosum*, *Shorea* and *Swintonia* (Srivastava *et al.*, 2014 and references therein). These taxa are found today in high rainfall regions either in the Western Ghats or in northeast India (Srivastava *et al.*, 2014). A good number of plant megafossils in the form of woods and leaves were described from Middle Siwaliks of Nalagarh and Jawalamukhi (Prasad, 2006). Middle Siwalik pollens and spores include *Cyathidites*, *Alsophilidites*, *Leptolepidites*, *Podocarpidites*, *Pinuspollenites*, *Monoporopollenites*, *Alnipollenites* and *Tetradomonoporites* (Rao and Verma, 2014 and references therein).

The typical Chinji lithology (Type area in Pakistan) of red beds occur around the famous primate yielding locality of Ramnagar. The mammalian fauna represents ~ 14 to 12 Ma (Sehgal and Patnaik, 2012; Parmar *et al.*, 2015). Ramnagar assemblage is very similar to the Chinji fauna and include rodents: *Kanisamys* cf. *potwarensis*, *Antemus chinjiensis*, *Megacricetodon* cf. *sivalensis* and *Sivacanthion complicatus*; primates: *Sivaladapis palaeindicus*, *Sivapithecus sivalensis*, *S. indicus* and *S. simonsi*; creodont: *Dissopsalis carnifex*; carnivores: *Eomellivora necrophila*, *Vishnuonyx chinjiensis*, *Amphicyon* sp., *Percrocuta carnifex*, *Viverra chinjiensis*, and *Vishnufelis* sp.; perissodactyls: cf. *Caementodon* sp. *Aceratherium perimense*, *Gaindatherium browni*, *Brachypotherium* sp., *Chilotherium?* *intermedium*, *Chalicotherium* sp.; proboscideans: *Deinotherium pentapotamiae*, *Prodeinotherium* sp., *Gomphotherium* sp. and *Tetralophodon* sp.; suids:

*Hippopotamodon haydeni*, *Conohyus chinjiensis*, *C. sindiense*, *Listriodon pentapotamiae*, *Propotamochoerus* sp. and *Sus* sp.; anthracotheres *Anthracootherium punjabiense*

(=*Microbunodon silistrensis*) and *Hemimeryx pusillus* (= *Merycopotamus pusillus*) (Lihaerou et al., 2004); tragulids: *Dorcabune anthracotherioides*, *D. nagrii*, *Dorcatherium majus*, *D. minus* and *D. Nagrii*; Pecora: *Progiraffa*; giraffids: *Giraffa priscilla* and *Giraffokeryx punjabiensis*; bovids: *Helicopotax*, *Gazella* and *Kubanotragus* (Patnaik, 2016 and references therein). Recent addition to the rodent fauna include *Megacricetodon daamsi*, *Megacricetodon sivalensis* and *Myocricetodon sivalensis* (Parmar et al., 2015). In the northeast the Garo Hills, Assam have yielded *Microbunodon silistrensis* suggesting a late early Miocene (17.8 Ma) to middle Miocene (11.4 Ma) age (Patnaik, 2016 and references therein).

### Late Miocene (11-5.5 Ma) Fauna and Vegetation

During the Late Miocene the global climate entered a phase of cooler and drier conditions. A sudden rise of the Himalayas and intensification of the Asian monsoons were mainly responsible for an overall change in the vegetation towards the dominance of C4 grasslands in the Indian subcontinent. The sedimentary environment of the Indian foreland also changed leading to the development of southward shifting inter-fan river system that replaced the large emergent rivers.

The floral assemblage of Middle Siwaliks of Nepal show presence of subtropical and temperate forests with high altitude taxa such as *Abies*, *Larix* and *Picea* (Hoorn et al., 2000). Middle Siwaliks exposed near Haridwar have yielded *Diospyros* belonging to Ebenaceae, *Homonioia* and *Croton* of Euphorbiaceae, *Albizia*, *Cassia*, *Dalbergia* and *Pongamia* of the Fabaceae, *Swietenia* of the Meliaceae, *Myrsine* of the Myrsinaceae, *Eucalyptus* of the Myrtaceae and *Zizyphus* of the Rhamnaceae families (Prasad and Khare, 1994).

The magnetostratigraphically dated Late Miocene Haritalyangar locality has yielded primates: *Indopithecus*, *Sivapithecus*, *Indraloris*, *Sivaladapis* and *Pliopithecus* (Patnaik, 2013 and references therein). The mammals that appear for the first time during this period include: *Parapelomys*, *Parapodemus*, *Miorhizomys*, *Sivaonyx*, *Ictitherium*, *Enhydrodon*, *Tetralophodon*, *Choerolophodon*, *Stegolophodon*, *Anancus*,

*Hipparion*, *Propotamochoerus*, *Sus*, *Giraffokeryx*, *Pachyportax*, *Bramatherium*, *Selenoportax* and *Vishnutherium*.

The Kalagarh locality, which is situated in the state of Uttarakhand has also yielded primates and other mammals. Patnaik (2013) constrained this locality between 9.3 and 8 Ma based on first and last appearances of Late Miocene mammals. Sharma and Patnaik (2014) recovered a fossil suid, namely *Tetraconodon* cf. *intermedius* from Baripada Beds exposed in the Mayurbhanj District of Orissa. Based on this find Sharma and Patnaik, (2014) place this site between 10-8 Ma.

Another well known Middle Siwalik locality is Nurpur, Himachal Pradesh that has yielded a fauna very similar to that of Haritalyangar. The Nurpur assemblage include *Dissopsalis*, *Amphicyon*, *Deinotherium*, *Prodeinotherium*, *Gomphotherium*, *Tetralophodon*, *Aceratherium*, *Gaindatherium*, *Cormhipparion*, *Hipparion*, *Hippopotamodon*, *Listriodon*, *Propotamochoerus*, *Anthracotherium*, *Merycopotamus*, *Dorcabune*, *Dorcatherium*, *Hydaspthierium*, *Giraffokeryx*, *Bramatherium* and *Protragocerus*. Patnaik (2013) suggested an age bracket of 10.1-9.7 Ma to this site. Recently, Sehgal (2015) described *Tetraconodon minor* and several other mammals from this site and discussed the Eurasian and African affinities and in situ evolution of these mammals.

Perim Island in the gulf of Gujarat has yielded a diverse assemblage of mammals including the proboscideans *Anancus perimense*, *Deinotherium angustidens*, *Gomphotherium hasnotensis*, *Stegolophodon cautleyi* and *Stegolophodon latidens*: the perissodactyls *Brachypotherium perimense*, *Aceratherium perimense* and *Hipparion antelopinum*: the artiodactyls *Dorcatherium minus*, *Bramatherium perimense*, *Antelope planicornis*, *Pachyportax* sp. *Tragoportax* sp. *Tragoceras perimense*, *Selenoportax vexillarius*, *Ruticeras compressa* and *Merycopotamus pusillus*. With an improved biochronology available for the Neogene bovids and equids such as *Hipparion antelopinum* these deposits would be younger than 10.7 Ma. Based on the presence of *Selenoportax vexillarius* these sediments would range between 10.2 and 9.8 Ma (See Patnaik, 2016).

Bokabil Formation in Tripura is known for proboscideans *Gomphotherium angustidens* and *Stegolophodon cautleyi*; the perissodactyl *Hipparion theobaldi*, the artiodactyls *Dorcatherium*, *Pachyportax* sp. and *Propotamochoerus hysudricus*. If we follow the first and last appearance of taxa such as *Hipparion* and *Propotamochoerus hysudricus* these deposits would be at least 6.8 Ma and at the most 10.2 Ma old (Patnaik, 2016).

### Pliocene (~ 5.3 to 2.6 Ma) Fauna and Vegetation

The Upper Siwaliks are characterised by thickly bedded conglomerate facies with lensoid bodies of sandstone and mudstones. However, the fine-grained facies belonging to Tatrot and Pinjor formations can be found around Jammu and Chandigarh.

The lower Pliocene Upper Siwalik sediments of Saketi area have yielded spores, gymnosperms and angiosperm pollen such as *Laricoidites*, *Inaperturopollenites*, *Pinuspollenites*, *Pinjoriapollis* and *Monoporopollenite*. Upper Siwalik sequence in the Haripur Khol area of Himachal Pradesh has produced pteridophytic spores of *Cyathea*, *Pteris*, *Ceratopteris*, *Lycopodium* and some Polypodiaceae spores and gymnosperms such as *Pinus* and *Abies* (Phadtare *et al.*, 1994). The angiosperms reported by Phadtare *et al.* (1994) include the true grasses (Poaceae), palms (Arecaceae), lilies (Liliaceae), custard apples (Annonaceae), goosefoots (Chenopodiaceae), bombax (Bombacaceae), sunflower (Asteraceae), mallows (Malvaceae), leguminose (Mimosaceae), water lilies (Nympheaceae), milkworts (Polygalaceae), bedstraws (Rubiaceae) and carrots (Apiaceae). Phadtare *et al.* (1994) found 4-3.5 Ma to be dominated by dry grasslands, 3.5-2.7 Ma had muddy and marshy conditions and between 2.7 and 2.5 Ma widespread ponding conditioned developed.

The Tatrot Formation in Pakistan represents 200,000 years from 3.5 to 3.3 Ma and has yielded *Anancus falconeri*, *Hippohyus lydekkeri*, *Hippotragus* and *Hydaspicobus* (Colbert, 1935; Pilgrim, 1939). The Lower Pliocene records in India are fragmentary. It is only at Saketi, Himachal Pradesh that we get some exposures of these sediments that have yielded some mammals. The mammalian species that have been recovered from Saketi are: the leporid

*Pliosivalagus whitei*, murines, *Dilatomys moginandensis*, *Cremnomys* cf. *C. cutchicus*, *Bandicota sivalensis* and *Golunda tatroticus*, the gerbelline *Abudhabia* cf. *A. kabulense*, elephants, *Stegodon insignis*, *Anancus* (= *Pentalophodon*) *khetpuraliensis*, the suids *Hippohyus tatroti*, *Sivachoerus* and *Propotamochoerus hysudricus*, the hippo, *Hexaprotodon sivalensis*, the giraffid, *Hydaspitherium megacephalum*, the equid *Hipparion* and the bovid *Gazella*.

In the Upper Pliocene sediments the Saketi region contain *Suncus* cf. *S. murinus*, *Pliosivalagus whitei*, *Rhizomyides saketiensis*, *Rhizomyides* cf. *R. sivalensis*, *Mus flynni*, *M. jacobsi*, *Parapelomys robertsi*, *Bandicota sivalensis*, *Cremnomys*, *Millardia*, *Anancus* (= *Pentalophodon*) *khetpuraliensis*, *Elephas planifrons*, *Stegodon insignis*, *Stegodon bombifrons*, *Hexaprotodon sivalensis*, *Sivachoerus*, *Hippohyus tatroti*, *Propotamochoerus hysudricus*, *Camelus sivalensis*, *Sivatherium giganteum*, *Proamphibos kashmiricus*, *Probison dehmi*, *Hydaspitherium megacephalum*, *Hipparion* and *Gazella* (Patnaik, 2013; Nanda, 2013).

Upper Pliocene sediments in the Jammu region have yielded *Golunda kelleri*, *Dilatomys pilgrimi*, *Rhizomyides sivalensis*, *Abudhabia* cf. *A. kabulense*, *Stegodon bombifrons*, *Hipparion antelopinum*, *Cormohipparion theobaldi* and *Propotamochoerus hysudricus* (Nanda, 2013).

A morpho-taxonomic study on leaf remains of 23 species and 20 genera belonging to 15 angiosperm families recorded from the upper part of the Siwalik succession of sediments (Kimin Formation; upper Pliocene to lower Pleistocene) of Papumpare district, Arunachal Pradesh, were compared with their NLRs (Nearest Living Relatives). Among these taxa, 11 species are recorded as new to the Neogene flora of India. Analysis of the floral assemblage with respect to the distribution pattern of modern equivalent taxa and the physiognomic characters of the fossil leaves, suggests that a tropical evergreen forest was growing in a warm humid climate in the region at the time of deposition. This is in contrast to modern tropical semi-evergreen forests that occupy the same area. Values of mean annual temperature (MAT) of 29.3°C and

mean annual precipitation (MAP) of 290 mm have been calculated using leaf-margin characters and fossil leaf size. The study shows that Upper Pliocene to lower Pleistocene was comparatively much more humid as compared to the Pliocene deposits of the Jammu region (Khan *et al.*, 2011).

## Discussions

Overall the Neogene faunal and vegetation changes follow the climate, tectonic and eustatic pattern. Just prior to the Neogene a cooler climate was present because of an increase in the polar ice (DeConto *et al.*, 2008; Zachos *et al.*, 2001). This also led to an overall drop in the sea level. The early Neogene saw an increase in temperature due to the closure of the Tethys leading to a reorganisation of ocean currents. This development culminated with the Middle Miocene Climate Optima. During this period a warm and humid condition prevailed and tropical evergreen forests covered a large part of the subcontinent. Among these were the dipterocarps, which extended from Myanmar in the east to Kutch and Kasauli in the West. By the later part of the Middle Miocene woodlands started spreading and there is evidence of seasonality, which by the Late Miocene gets intensified and monsoonal conditions prevailed. This led to a dominance of the grasslands in place of the forests. Warm and humid conditions continued throughout the Pliocene when the landscape was dominated by wooded grasslands. The Late Pliocene saw cooler and drier conditions.

Among the mammals the Laurasiatheres which include the Artiodactyls, perissodactyls, bats, carnivores and pangolins (O'Leary *et al.*, 2013) were already present in Eurasia in the early Neogene. In fact, perissodactyls were present on the Indian plate as early as Eocene prior to its collision with Asia (Bajpai *et al.*, 2006; Rose *et al.*, 2014). On the other hand the Afrotheres that includes the proboscideans, hyrcooids, and embrithopods were confined to Africa till the latest Oligocene. But around the Oligo-Miocene boundary ~ 23 Ma tectonics led to the suturing of Afro-Arabian and Eurasian plates. This land connection permitted Eurasian mammals to disperse into Africa and African mammals to move into Eurasia. This land connection known as the "Gomphotherium Land Bridge" facilitated African proboscideans in the early Miocene (~20 Ma) to enter the subcontinent

and also disperse into Europe and finally into North America through the Bering Strait. Taking advantage of this route Eurasian mammals such as rhinos, chalicotheres and suids dispersed into Africa between 20-18 Ma (Bernor *et al.*, 1987; Bishop, 2010; Coombs and Cote, 2010). Among the proboscideans *Prodeinotherium* and *Gomphotherium* were the first to cross the Afro-Arabia-Eurasia land bridge and reach the Indian subcontinent. Flynn *et al.*, 2013 proposed the First Appearance Datum of *Prodeinotherium* at ~ 23 Ma, whereas *Gomphotherium* now occurs at ~ 22 Ma, suggesting an earlier dispersal of these two taxa (Antoine *et al.*, 2013 and reference therein).

The existence of tragulid *Dorcatherium* in Kenya and Chitarwata Formation of Pakistan may indicate an early Miocene faunal exchange between India and Africa (Antoine *et al.*, 2013). There is good evidence of presence of south asian murid close to *Potwarmus* and the ctenodactylid *Sayimys* ~ 18.5 Ma in Saudi Arabia and North Africa (Flynn and Wessels, 2013 and references there in). Likewise, the rhizomyine *Prokanisamys* also disperses to Saudi Arabia and North Africa in the early Miocene. In the Middle Miocene rodents such as *Democricetodon*, *Eumayrion*, *Sayimys* and *Myocricetodon* are found in Anatolia suggesting migration (Flynn and Wessels, 2013). *Primus* and *Megacricetodon* of an East Asian origin entered the subcontinent in the early Miocene (Flynn *et al.*, 2014).

Since the earliest creodonts are found in Africa, the creodonts *Hyanailouros* and *Pterodon* might have migrated from Africa to Asia at ~18 and 19.5 Ma followed by *Dissopsalis* that appears for the first time in the Siwaliks at 16.1 Ma. On the other hand fossil record suggest that the carnivores migrated from Asia to Africa. One good example of this is the early record of the carnivore, *Amphicyon* in the earliest Miocene sediments of Bugti Hills and its later occurrence in Africa (Antoine *et al.*, 2013). Around this time (16 Ma) the thryonomyid *Kochalia* also reaches Pakistan from Africa (Flynn and Winkler, 1994). The primate *Dionysopithecus* could be another early immigrant from Africa to the subcontinent. The anthracotheres entered Africa from Asia in the Early Miocene as well.

The Middle Miocene saw dispersal of Apes



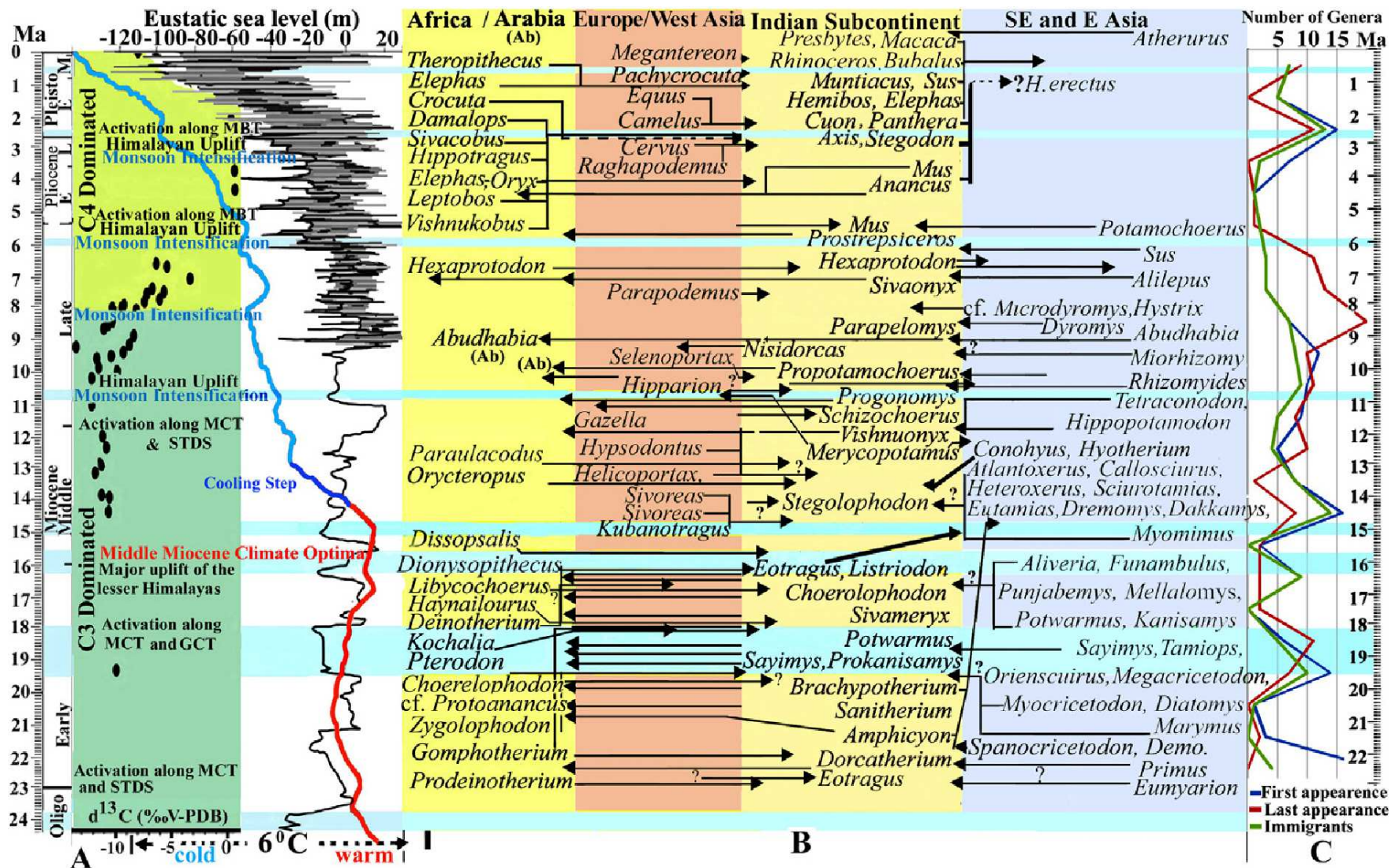


Fig. 2: A correlation between Neogene-Quaternary global temperature, sea levels and subcontinental tectonics and vegetation and mammalian faunal changes. A: Vegetation change based on mammalian enamel carbon stable isotope values (Martin *et al.*, 2011 and references therein); eustatic sea levels (Miller *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 (source: Patnaik, 2016)

prior to 16 Ma, these were not present in Eurasia. At the start of Middle Miocene, seasonal forests and woodlands expanded in both Africa and Eurasia. The early apes most likely adapted to such open conditions dispersed to Europe and then to the subcontinent. The Siwalik Miocene ape such as *Sivapithecus* most likely had its ancestor reaching the Indian subcontinent from the west sometime around 15-16 Ma (Begun, 2005).

During the Late Miocene the climate became cooler and drier facilitating the spread of grasslands at the expense of forests. The three toed equid *Hipparion* disperses from North America in the Middle Miocene arriving first in China around and then in Europe followed by in the Siwaliks at 10.7 Ma (Barry *et al.*, 2002). The bovid *Kobus porrecticornis* ranges in Pakistan from 8.1 to 7.7 Ma (Gentry *et al.*, 2014). Bibi (2011) found that *Kobus porrecticornis* indicates intercontinental dispersal as it is known from the latest Miocene of East and South Africa between 6.5 to 5 Ma. Another bovid *Prostrepsiceros vinayaki* ranged in the Siwaliks from 9.3-7.9 Ma, and has been recorded from Arabia around 8-6 Ma and in Africa between 5.7 and 5.4 Ma, again indicating existence of dispersal corridor in the Late Miocene (Bibi, 2011). The widespread suid *Propotamochoerus hysudricus* is an immigrant at ~ 10 Ma to the subcontinent (Flynn *et al.*, 2014) and most probably came from China where the genus occurs in older deposits. It also occurs at Abu Dhabi sometime between 8-6 Ma (see Patnaik, 2016 and reference therein).

A faunal event known as the 'Leporid Event' happens in the late Miocene (Flynn *et al.*, 2013). The first leporid *Alilepus* appears in south Asia at 7.4 Ma from North America via China and go on to disperse into Africa (Flynn *et al.*, 2013). The porcupine *Hystrix* appears for the first time at 8 Ma in south Asia arriving most likely from the east (Flynn and Wessels, 2013). The gerbil *Abudhabia* was widespread and is known from Late Miocene of China, Pakistan, Afghanistan, UAE, Libya and Kenya (Flynn and Wessels, 2013; Fortelius, 2013 NOWdatabase). The otter *Sivaonyx* was widespread too occurring in India, Pakistan, China, Thailand, Turkey and Germany during Middle to Late Miocene. It most likely dispersed to Africa in the Late Miocene (Grohe *et al.*, 2013).

During the Early Pliocene murid rodents of south asian origin such as *Mus* appears in Kenya (Patnaik, 2014) where as *Golunda* group murids occur at Early Pliocene of Morocco and Ethiopia (Fortelius, 2013 NOW database). The hippo *Hexaprotodon sivalensis* and the elephant *Elephas planifrons* were also immigrants to the subcontinent from Africa. *Camelus*, *Equus*, Cervids and *Rhagapodemus* dispersed to the subcontinent in the Late Pliocene (Kotlia, 2013; Patnaik, 2016 and references therein).

Spatial variation in climate was seen during later part of Neogene. Plant records show that Late Pliocene of Arunachal Pradesh was comparatively much more humid (Khan *et al.*, 2011) as compared to the Late Pliocene of the Jammu region.

Overall, the major dispersal events that include number of first and last appearances and immigrants, coincides with major sea-level drops (Miller *et al.*, 2005) (Fig. 2).

## Conclusions

Climate played a major role in the distribution of fauna and flora of the Indian subcontinent throughout the Neogene. Tectonics led to the closure of the Tethys followed by the collision of Africa and Eurasia, which in turn created land connections and altered the climatic and vegetation scenario of the subcontinent. Combined with this, major sea level drops allowed faunal and floral elements to disperse into and out of the subcontinent. Most of the mammalian dispersals from and to the west (Africa, Eurasia), first and last appearances took place around 20-18, 17-16, 11-10, 6-5 and 3-1 Ma. Neogene mammals appears to have followed a coastal route to disperse into the subcontinent, as most of the early Neogene sites such as Chitarwata, Kargil and Kutch have yielded coastal flora and fauna. The large mammalian data indicate that most of the migrations took place from the Africa, West Asia and Europe. However, several small mammals entered the subcontinent from Myanmar, Thailand and South China.

## Acknowledgements

We would like to thank Professors A K Singhvi and D M Banerjee for the invitation to contribute to this volume.



## References

- Antoine P O, Métais G, Orliac M, Crochet J Y, Flynn L J, Marivaux L, Rajpar A R, Roohi G and Welcomme J L (2013) *Mammalian Neogene biostratigraphy of the Sulaiman Province, Pakistan*. In: Wang, X, Flynn L J, Fortelius, M (Eds.), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology* Columbia University Press, New York, pp 400-422
- Antoine P O, Downing K F, Crochet J Y, Duranthon F, Flynn L J, Marivaux L, Métais G, Rajpar A R and Roohi G (2010) A revision of *Aceratherium blanfordi* Lydekker, 1884 (Mammalia: Rhinocerotidae) from the early Miocene of Pakistan: postcranials as a key *Zoological Journal of the Linnean Society* **160** 139-194
- Bajpai S, Kapur V V, Thewissen J G M, Das D P and Tiwari B N (2006) New early Eocene cambaythere (Perissodactyla, Mammalia) from the Vastan Lignite Mine (Gujarat, India) and an evaluation of cambaythere relationships *Journal of the Palaeontological Society of India* **51** 101-110
- Barry J C, Behrensmeyer A K, Badgley C E, Flynn L J, Peltonen H, Cheema I U, Pilbeam D, Lindsay E H, Raza S M, Rajpar A R and Morgan M E (2013) *The Neogene Siwaliks of the Potwar Plateau, Pakistan*. In: Wang X, Flynn L J, Fortelius M (Eds.), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology* Columbia University Press, New York, pp 373-399
- Barry J C, Morgan M E, Flynn L J, Pilbeam D, Behrensmeyer A K, Raza S M, Khan I A, Badgley C, Hicks J and Kelley J (2002) Faunal and environmental change in the late Miocene Siwaliks of northern Pakistan *Paleobiology* **28** 1-71
- Begun D R (2005) *Sivapithecus* is east and *Dryopithecus* is west, and never the twain shall meet *Anthropol Sci* **113** 53-64
- Bernor R L, Brunet M, Ginsburg L, Mein P, Pickford M, Rögl F, Sen S, Steininger F and Thomas H (1987) A consideration of some major topics concerning Old World Miocene mammalian chronology, migrations and paleogeography *Geobios* **20** 431-439
- Bhandari A, Mohabey D M, Bajpai S, Tiwari B N and Pickford M (2010) Early Miocene mammals from central Kutch (Gujarat) western India: Implications for geochronology, biogeography, eustacy and intercontinental dispersals *Neues Jahrbuch Fur Geologie Palaontologie Abhandlungen* **256** 69-97
- Bhandari A, Pickford M and Tiwari B N (2015) Basal Late Miocene Mammal Fauna from Tapar and Pasuda, *Kachchh Münchner Geowissenschaftliche Abhandlungen Reihe A: Geologie und Paläontologie* **4** 31-38
- Bibi F (2011) Mio-Pliocene faunal exchanges and African biogeography *The record of fossil bovids* PLoS ONE **6**:e16688
- Bishop L C (2010) Suoidea In: Werdelin L and Sanders W J (Eds) *Cenozoic Mammals of Africa* University of California Press, Berkeley, pp 821-842
- Colbert E H (1935) Siwalik mammals in the American Museum of Natural History *Transactions of the American Philosophical Society* **26** 278-294
- Coombs M C and Cote S M (2010) *Chalicotheriidae* In: Werdelin L and Sanders W J (Eds.) *Cenozoic Mammals of Africa*. University of California Press, Berkeley, pp 659-668
- DeConto R M, Pollard D, Wilson P A, Palike H, Lear C H, Pagani M (2008) Thresholds for Cenozoic bipolar glaciations *Nature* **455** 652-656
- Dutta S, Tripathi S K M, Mallik M, Mathews R P, Greenwood P F, Malagalapalli R R and Summons E (2011b) Eocene out-of-India dispersal of Asian dipterocarps *Review of Palaeobotany & Palynology* **116** 63-68
- Flynn L J, Lindsay E H, Pilbeam D, Raza S M, Morgan M E, Barry J C, Badgley C, Behrensmeyer A K, Cheema I U, Rajpar A R and Opdyke N D (2013) The Siwaliks and Neogene evolutionary biology in South Asia. In: Wang X, Flynn L J, Fortelius M (Eds.), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology*. Columbia University Press, New York, pp 353-372
- Flynn L J and Wessels W (2013) *Paleobiogeography and South Asian Small mammals. Neogene Latitudinal faunal Variation* The Siwaliks and Neogene evolutionary biology in South Asia. In: Wang X, Flynn L J, Fortelius M (Eds.), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology*. Columbia University Press, New York, pp. 445-460
- Flynn L J, Morgan M E, Pilbeam D and Barry J (2014) "Endemism" relative to space, time, and taxonomic level *Annales Zoologici Fennici* **51** 245-258
- Flynn L J and Winkler A J (1994) Dispersalist implications of *Paraulacodus indicus*: a South Asian rodent of African affinity *Historical Biology* **9** 223-235
- Fortelius M (2013) *New and Old Worlds Database of Fossil Mammals (NOW)* University of Helsinki, (<http://www.helsinki.fi/science/now/>)
- Gentry A W, Solounias N and Barry J C (2014) Stability in higher level taxonomy of Miocene bovid faunas of the Siwaliks *Annales Zoologici Fennici* **51** 49-56
- Guleria J S, Thakur V C, Virdi N S and Lakhnpal R N (1983) A fossil wood of *Prunus* from Kargil (=Liyan) Formation of Ladakh. In: Thakur, V.C., Sharma, K.K. (Eds.), *Geology of Indus Suture Zone of Ladakh, WIHG, Dehradun*, pp.

- 187-193
- Grohé, Camille Bonis, Louis de Chaimanee, Yaowalak, Blondel, Cécile, Jaeger and Jean-Jacques (2013) The oldest Asian *Sivaonyx* (Lutrinae, Mustelidae): a contribution to the evolutionary history of bunodont otters *Palaeontologia Electronica* **16** 30A 13
- Hoorn C, Ohja T and Quade J (2000) Palynological evidence for vegetation development and climatic change in the Sub-Himalayan Zone (Neogene, Central Nepal) *Palaeogeography, Palaeoclimatology, Palaeoecology* **163** 133-161
- Khan MA, Ghosh R, Bera S, Spicer RA and Spicer TE V (2011) Floral diversity during Plio-Pleistocene Siwalik sedimentation (Kimin Formation) in Arunachal Pradesh, India and its palaeoclimatic significance *Palaeobiodiversity and Palaeoenvironments (Springer Publ)* **91** 237-255
- Kotlia B S (2013) *Rhagapodemus* (Rodentia, Mammalia) from the Karewas of Kashmir (India): another evidence of Pliocene faunal exchange between Europe and NW India *Himalayan Geology* **34** 1-8
- Kumar K and Kad S (2003) Early Miocene vertebrates from the Murree Group, northwest Himalaya, India affinities and age implications *Himalayan Geology* **24** 29-53
- Lihoreau F, Barry J, Blondel C and Brunet M (2004) A new species of Anthracotheriidae, *Merycopotamus medioximus*, nov. sp. from the Late Miocene of the Potwar Plateau, Pakistan *Comptes Rendus Palevol* **3** 653-662
- Martin C, Bentaleb I and Antoine P O (2011) Pakistan mammal tooth stable isotopes show paleoclimatic and paleoenvironmental changes since the early Oligocene *Palaeogeography, Palaeoclimatology, Palaeoecology* **31** 19-29
- Miller K G, Kominz M A, Browning J V, Wright J D, Mountain G S, Katz M E, Sugarman P J, Cramer B S, Christie-Blick N P and Stephen F (2005) The Phanerozoic Record of Global Sea-Level Change *Science* **310** 1295-1298
- Nanda A C (2013) Upper Siwalik Mammalian Faunas of the Himalayan foothills *Journal of the Palaeontological Society of India* **58** 75-86
- O'Leary MA, Bloch J I, Flynn J J, Gaudin T J, Giallombardo A, Giannini N P, Goldberg S L, Kraatz B P, Luo Z X, Meng J, Ni X, Novacek M J, Perini F A, Randall Z S, Rougier G W, Sargis E J, Silcox M T, Simmons N B, Spaulding M, Velazco P M, Weksler M, Wible J R and Cirranello A L (2013) The placental mammal ancestor and the post-K-Pg radiation of placentals *Science* **339** 662-667
- Parmar V, Prasad G V R, Kumar J, Malik M A and Rigzin N (2015) *Cricetid rodents from the Lower Siwalik Subgroup of Jammu, India: Biochronological Significance*. Paleoworld (in press)
- Patnaik R (2016) Neogene-Quaternary Mammalian Paleobiogeography of the Indian Subcontinent: An appraisal *Comptes Rendus Palevol* **919** 1-14
- Patnaik R (2013) *Indian Neogene Siwalik mammalian biostratigraphy: An overview* In: Wang X, Flynn L J, Fortelius M (Eds.), Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology. Columbia University Press, New York, pp. 423-444
- Patnaik R (2014) Phylogeny Of Siwalik Murine Rodents: Implications For *Mus-Rattus* Divergence Time *Journal of Palaeontological Society of India* **59** 15-28
- Patnaik R, Milankumar K, Negi S, Williams L, Kay B and Chatrath R P (2014) Additional Vertebrate Remains from the Early Miocene of Kutch, Gujarat *Special Publication of The Palaeontological Society of India* **5** 353-365
- Phadtare N R, Kumar R and Ghosh S K (1994) Stratigraphic palynology, floristic succession and the Tatrot/Pinjur boundary in Upper Siwalik sediments of Haripur Khol area, district, Sirmaur (Himachal Pradesh), India *Himalayan Geology* **15** 69-82
- Pilgrim G E (1939) The fossil Bovidae of India *Palaeontologia Indica NS* **26** 1-356
- Prasad M (2006) Plant fossils from Siwalik sediments of Himachal Pradesh and their palaeoclimatic significance *Phytomorphology* **56** 9-22
- Prasad M and Khare E G (1994) Occurrence of *Dipterocarpus* Gaertn. in the Siwalik sediments of Hardwar, Uttar Pradesh, India *Biological Memoirs* **20** 51-54
- Prasad G V R, Bajpai S, Singh S and Parmar V (2005) First cricetid rodent (Mammalia) from the Ladakh Molasse, Northwestern Himalaya, India: age implications *Himalayan Geology* **26** 85-92
- Rose Kenneth D, Holbrook, Luke T. Rana, Rajendra S, Kumar, Kishor, Jones, Katrina E, Ahrens, Heather E, Missiaen, Pieter, Sahni, Ashok, Smith and Thierry (2014) Early Eocene fossils suggest that the mammalian order Perissodactyla originated in India *Nature Communications* **5** 5570 DOI: 10.1038/ncomms6570
- Rao M R and Verma P (2014) Miocene Palynology in India: Present Status and Future Prospect *Special Publication of the Palaeontological Society of India* **5** 145-160
- Rust J, Singh H, Rana R S, Mccann T, Singh L, Anderson K and Sarkar N (2010) Biogeographic and evolutionary implications of a diverse paleobiota in amber from the early Eocene of India *Proceedings of the National Academy of Sciences USA* **107** 18360-18365

- Sehgal R K and Patnaik R (2012) New muroid rodent and *Sivapithecus* dental remains from the Lower Siwalik deposits of Ramnagar (J&K, India): Age implication *Quaternary International* **269** 69-73
- Sehgal R K (2015) Mammalian faunas from the Siwalik sediments exposed around Nurpur, District Kangra (H.P.): age and palaeobiogeographic implications *Himalayan Geology* **36** 9-22
- Sharma K Milankumar and Patnaik R (2013) Record of Late Miocene Suid, *Tetraconodon intermedius* from Baripada Beds (Mayurbhanj, Orissa): Age Implications *Journal of Palaeontological Society of India* **58** 213-218
- Shukla A, Mehrotra R C and Guleria J S (2013) Emergence and extinction of Dipterocarpaceae in western India with reference to climate change: Fossil wood evidences *Journal Earth System Science* **122** 1373-1386
- Shukla A, Mehrotra R C, Mandal N and Thakkar M G (2015) Two new fossil woods from the early Miocene of Kutch, Gujarat, India and their significance *Historical Biology* **27** 970-977
- Srivastava, Gaurav, Mehrotra R C, Shukla A and Tiwari R P (2014) Miocene Vegetation And Climate In Extra Peninsular India: Megafossil Evidences. Special Publication of *The Palaeontological Society of India* **5** 283-290
- Tiwari B N, Verma B C and Bhandari A (2006) Record of Prodeinotherium (Proboscidea: mammalian) from the mid-Tertiary Dharamsala Group of the Kangra Valley, NW Himalaya, India: Biochronologic and palaeo-geographic implications *Jour Palaeontol Soc India* **51** 93-100
- Tiwari R P, Mehrotra R C, Srivastava G and Shukla A (2012) The vegetation and climate of a Neogene petrified wood forest of Mizoram, India *Journal of Asian Earth Sciences* **61** 143-165
- Tiwari R P, Ralte V Z, Zoramthara C, Srivastava G, Mehrotra R C, Paul S and Dutta S (2015) Fossil Leaves in Amber from the Bhuban Formation, Mizoram, India *Himalayan Geology* **36** 33-38
- Welcomme J L, Benammi M, Crochet J Y, Marivaux L, Métais G, Antoine P O and Baloch I S (2001) Himalayan Forelands: palaeontological evidence for Oligocene detrital deposits in the Bugti Hills (Balochistan, Pakistan) *Geological Magazine* **138** 397-405
- Zachos J C, Pagani M, Sloan L, Thomas E and Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present *Science* **292** 686-693.