

Biotic perspective of the Deccan volcanism and India–Asia collision: Recent advances

SUNIL BAJPAI

*Department of Earth Sciences, Indian Institute of Technology, Roorkee 247 667, India.
e-mail: sunilfes@iitr.ernet.in*

India's physical and biotic links after its separation from the former assembly of southern continents (Gondwanaland) continue to evoke global interest. Of particular interest is the period from 65 to 45 million years before present, which spans the interval from the terminal phase of India's northward flight as an isolated landmass until its collision with Asia. The faunal response during this period has had profound influence on origins, evolution and the distribution of many of the modern life forms. Recent fossil data from the Deccan intertrappean deposits of peninsular India have revealed extensive endemism among the freshwater ostracods, suggesting India's significant physical isolation around the Cretaceous–Tertiary (K–T) boundary (65 Ma), consistent with the geophysical data. The co-existence of Laurasian elements in the Deccan intertrappeans is now better explained in terms of transoceanic (sweepstakes) dispersal rather than the previously proposed direct terrestrial contact between India and Asia near the K–T boundary. Furthermore, the Deccan Traps volcanism has now been shown to be a major cause of the faunal extinctions, including that of dinosaurs, at the K–T boundary. New data from sections near Rajahmundry in the Krishna–Godavari Basin of southeastern India, and Jhilmili, in the Chhindwara district of central India, show that the end of the most massive phase of Deccan volcanism occurred at or near the K–T mass extinctions, demonstrating a cause and effect relationship. Data from Jhilmili also reveal a major marine seaway that existed across India during the K–T transition. This seaway, with major implications for the paleogeography, evolution and biotic diversity during the K–T transition, may possibly have followed the Narmada and Tapti rift zones. Following the Deccan eruptions, the most profound biotic events occurred around the time of India–Asia collision at ~55 Ma, which include the sudden appearance of several new mammalian taxa in the Indian subcontinent, as well as the dispersal of ancient Gondwanan taxa to the northern continents (the *Out-of-India* hypothesis). Recent fossil finds from Gujarat and the Himalaya have established the Indian subcontinent as the centre of origin/early evolution of several major groups of modern mammals, both marine and terrestrial, such as whales, primates, lagomorphs and hoofed mammals including horses.

1. Introduction

India's physical and biotic links following its break-up from the Gondwana Supercontinent continue to be a subject of intense debate (Briggs 1989, 2003; Sahni and Bajpai 1991; Chatterjee 1992; Thewissen and McKenna 1992; McKenna 1995; Prasad *et al* 1995; Chatterjee and Scotese 1999; Prasad and Sahni 1999; Whatley and Bajpai 2000,

2006; Case 2002; Rage 2003; Rana and Wilson 2003; Sahni 2006; Ali and Aitchison 2008; Sahni and Prasad 2008). The interval from 65 to 45 Ma during India's geodynamic evolution is of particular interest from a biotic perspective because of two major events that occurred during this period: the massive Deccan Traps volcanism in peninsular India at 65 Ma, and the initiation of India–Asia collision that is generally dated at

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ca. 55 Ma. For this reason, the Late Cretaceous – Early Eocene terrestrial vertebrate assemblages have an important bearing on our understanding of the degree of isolation of the Indian subcontinent and the resulting endemism, and possible dispersal routes during this time. Investigations carried out so far have revealed that India's latest Cretaceous (Maastrichtian) biota represents three distinct biogeographic domains: Gondwanan, Laurasian and the recently recognized endemic component. These components present major biogeographic puzzles and have led to hypotheses that basically underscore the fact that the distribution of terrestrial fossil biota, when considered in a rigorous phylogenetic and geodynamic context, can be a powerful tool for reconstructing past geographic relationships between landmasses.

This paper provides an overview of recent researches on the Indian late Cretaceous – Eocene faunas encompassing the interval from 65 to 45 Ma, with emphasis on the role of the Deccan Traps volcanism on the extinctions and paleogeography at the Cretaceous–Tertiary (K–T) boundary at 65 Ma, and the subsequent origin, evolution and dispersal of biota in the wake of the India–Asia collision at ca. 55 Ma.

2. India during the Cretaceous–Tertiary (K–T) transition (~65 Ma)

2.1 Biogeographic aspects

Traditional plate tectonic models depict India as an island continent during the late Cretaceous as the Indian plate drifted northwards through the middle of the Neotethys after its separation from Madagascar around 90 Ma until the India–Asia collision at ca. 55 Ma (e.g., Storey *et al* 1995). Such prolonged periods of physical isolation as an island continent should have resulted in a peculiar, endemic late Cretaceous biota without close affinities to contemporary faunas of other regions. However, the 'island continent' hypothesis has been contested by a number of paleontologists who argued that the terminal Cretaceous (Maastrichtian) terrestrial biota found in the Deccan intertrappean deposits of peninsular India do not provide any evidence of endemism (e.g., Sahni 1984). Indeed, during the past over two decades, investigations of the terminal Cretaceous Deccan intertrappean biota have revealed an admixture of Laurasian (e.g., Jaeger *et al* 1989; Sahni and Bajpai 1991; Prasad and Sahni 1999), Gondwanan (e.g., Krause *et al* 1997; Prasad and Sahni 1999; Sahni and Prasad 2008) and, more recently, endemic (Whatley and Bajpai 2006) components. In what follows, the biogeographic

implications of each of these components are discussed.

2.1.1 Laurasian elements

During the past more than two decades, a number of supposed Laurasian elements belonging to diverse faunal and floral groups have been identified in the latest Cretaceous (Maastrichtian) Deccan intertrappean deposits of peninsular India (e.g., Sahni and Bajpai 1991). The Laurasian taxa include discoglossid and pelobatid frogs, anguillid lizards and eutherian mammals. Frogs are particularly intolerant of saltwater and therefore appear to provide the most compelling evidence (e.g., Prasad and Rage 2004). It should be noted, however, that doubts have been cast in the past regarding the biogeographic significance of these and other Laurasian elements. Thewissen and McKenna (1992) noted that the Discoglossidae comprise a paraphyletic assemblage of primitive frogs, and Thewissen and McKenna (1992) doubted the familial attribution of *Deccanolestes* (Palaeoryctidae) on account of the fragmentary material on which this taxon was based. However, a recent phylogenetic study (Wible *et al* 2007) shows *Deccanolestes* to be phylogenetically nested within the Asian clades, which reinforces its biogeographic significance, as originally proposed by Prasad and Sahni (1988).

The presence of Laurasian taxa in the late Cretaceous intertrappean beds has long been considered inconsistent with most geophysical models that show the Indian subcontinent as an isolated landmass during this period. To explain this biogeographic anomaly, a number of biogeographic hypotheses have been discussed (Rana and Wilson 2003). These include: a direct contact between India and Asia as early as the K–T boundary at 65 Ma (Jaeger *et al* 1989; Prasad and Sahni 1999; Rage 2003); an extended northeastern Africa ('Greater Somalia') (Chatterjee and Scotese 1999) or an India tracking close to Africa during its northward movement (Briggs 2003). Most recently, the occurrence of Laurasian elements has been explained in terms of 'sweepstake' mode (i.e., through transoceanic rafting) from Asia to India, possibly aided by the Dras–Kohistan island arc system (Ali and Aitchison 2008; Sahni and Prasad 2008). The sweepstakes mechanism is most consistent with the available geophysical and geological data and it obviates the need to invoke a direct terrestrial connection between India and Asia at the K–T time. A long standing conflict between the paleontological and geophysical interpretations is thus reconciled. A similar transoceanic mode of dispersal has been proposed recently to explain the puzzling presence of several African elements in Madagascar (e.g., Vences *et al* 2004).

2.1.2 Gondwanan elements

Besides the Laurasian elements, the late Cretaceous terrestrial biota of India includes several Gondwanan taxa. Recent studies argue that the Gondwanan mammals and abelisaurid dinosaurs from late Cretaceous of Deccan intertrappean/Lameta Formation India exhibit close affinities to South American and Madagascan forms (Krause *et al* 1997; Sampson *et al* 1998; Wilson *et al* 2003). Gondwanan affinities are also suggested by the baurusuchid crocodiles from Baluchistan, Pakistan (Wilson *et al* 2001). In addition, haramyid mammals, *Indobatrachus* (Myobatrachinae), leptodactylid, hylid and ranoid frogs, nigerophiid and madtsoiid snakes, pelomedusoid turtles have also been cited in support of the Gondwanan connection (Sahni and Prasad 2008). The recent discovery in the late Cretaceous of Madagascar of a giant frog related to South American hyloids of the clade Ceratophryinae provides further evidence in favour of terrestrial links between Indo-Madagascar and South America until the late Cretaceous. Initially, Sahni (1984) proposed that some aseismic structures in the Indian Ocean such as the Mascarene Plateau and the Chagos-Laccadive ridges may possibly have served as a terrestrial route to allow faunal exchanges between India, Madagascar and South America during Maastrichtian. While most of the small-sized Gondwanan elements could have dispersed to India through the sweepstake mode, this mechanism cannot explain the presence of abelisaurid dinosaurs in India and baurusuchid crocodiles in Baluchistan. These two groups provide the most compelling evidence in favour of terrestrial links between the Indian subcontinent and South America during the late Cretaceous. Recent proposals suggest that such physical links existed between Indo-Madagascar-Seychelles block and South America during the late Cretaceous, but probably no later than 80 Ma (Krause *et al* 1997; Prasad and Sahni 1999; Ali and Aitchison 2008). Opinion is currently divided as to the exact dispersal route (*via* Kerguelen Plateau or Gunnerus Ridge) (see Hay *et al* 1999; Case 2002). Most recently, however, Ali and Aitchison (2009) argued that the idea of land connections between the East Antarctica and Indo-Madagascar *via* the Kerguelen Plateau is not tenable because this plateau was separated by extensive, deep marine barriers. These authors support a more direct South America to Madagascar-India passage through West and Central Africa, as proposed by Sereno *et al* (2004).

In any case, an isolated Indian landmass during the 15 million year period between 80 and 65 Ma should yield evidence of significant endemism. This

hypothesis cannot be currently tested because terrestrial biota from much of this interval is missing from the Indian fossil record. However, as discussed below, data on the late Maastrichtian fresh water ostracods from the Deccan intertrappeans is consistent with geophysical models indicating oceanic isolation during 80–65 Ma.

2.1.3 Endemic elements

As mentioned earlier, evidence for endemism among the Maastrichtian-Paleocene terrestrial faunas of India was lacking until recently, and this led to notions of India's biological (and physical) connectivity with the surrounding landmasses in the Indian Ocean during this interval (e.g., Sahni 1984). Recently, however, in a series of publications, extensive endemism has been recognized among Maastrichtian-early Paleocene freshwater ostracod faunas of the Deccan intertrappean deposits (Whatley and Bajpai 2006 and references therein; Sharma *et al* 2008). The intertrappean ostracod assemblage is remarkably diverse and, comprises over 75 freshwater ostracod species which are endemic (*Indian*) at species level. At the generic level, the intertrappean ostracods are cosmopolitan and show nearly as much affinity with European and North American Cretaceous ostracods as they do with other Asian faunas (Whatley and Bajpai 2000, 2006). However, it is surprising that in spite of India's erstwhile relations with the Gondwana continents, the degree of similarity of intertrappean ostracod faunas to their African counterparts is extremely low, both at specific and generic level. Dissimilarity is also apparent between the Deccan intertrappean and South American ostracod faunas.

Thus, the ostracod endemism recently documented from the Deccan intertrappeans contradicts previous notions of their close Chinese/Mongolian affinities. Given that ostracods have an extraordinary dispersal advantage (parthenogenetic reproduction, dessication/freezing resistant eggs capable of long distance wind dispersal), the extensive endemism recognized, is remarkable and supports geophysical models that show India as an isolated landmass around the K-T boundary (figure 1). Migration of Asian taxa (e.g., pelobatid and discoglossid frogs, eutherian mammals) to India at this time most likely involved transoceanic (sweepstake) dispersal, and not a continuous land route as previously proposed (e.g., Rage 2003).

2.2 Deccan Traps volcanism and its role in the K-T extinctions

The Deccan Volcanic Province (DVP) of peninsular India represents one of the largest occurrences

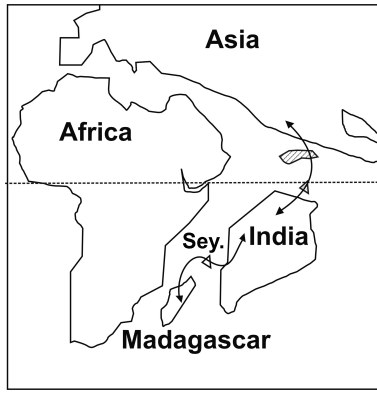


Figure 1. Paleogeographic model showing India's physical isolation around 65 Ma. Arrows indicate biotic exchanges through the process of transoceanic (sweepstakes) dispersal (modified after Ali and Aitchison 2008).

of continental flood basalt eruptions in the Earth's history. During the past two decades or so, there has been a dramatic revival of interest in this massive volcanic activity primarily because of its coincidence with the K–T boundary mass extinctions at 65 Ma, as revealed by a wealth of radiometric and palaeomagnetic data (e.g., Chenet *et al* 2007 and references therein). In addition, modeling of deleterious consequences of the Deccan volcanism in terms of toxic gases that would have been injected into K–T atmosphere show, for example, that the volume of SO₂ emitted by large individual eruptions could be similar to that released by the Chicxulub impact, and that each of these eruptions may have injected 10 to 100 times more SO₂ in the atmosphere than the historic 1783 Laki eruption (Chenet *et al* 2005; Self *et al* 2008). These studies highlight the role of Deccan volcanism in the global climate change at the K–T, and by implication, in the faunal and floral mass extinctions, including that of dinosaurs. However, a clear link between volcanism, climate and extinctions has remained elusive until recently because of our lack of knowledge regarding the precise position of the K–T extinction level in the Deccan volcanic pile. Major advances have been made during the past few years in our understanding of the duration of Deccan volcanism, its relevance to the global debate on K–T boundary extinctions and India's paleogeography during the eruptions.

2.2.1 *Timing and duration of Deccan volcanism*

In the past, biostratigraphic age determination of intertrappean sediments for the main part of the Deccan volcanic province, has generally been difficult because these sediments mostly yield terrestrial fossils which, though diverse, are not age-diagnostic (e.g., Khosla and Sahni 2003).

Initially, the Deccan intertrappeans were generally considered to be early Tertiary (Paleocene) in age based mainly on paleobotanical data, especially plant megafossils and charophytes (see Bande *et al* 1988 for a review). During the past two decades or so, the presence of dinosaur fossils (eggshell fragments, teeth and rare bones) in several intertrappean localities led to the general acceptance of a Maastrichtian age for these deposits (e.g., Sahni and Bajpai 1988; Srinivasan 1996; Bajpai and Prasad 2000).

The precise position of the K–T boundary in the Deccan volcanic pile has long been elusive and has precluded a clear link between volcanism, climate and extinctions. Most recently, biostratigraphic data from southeastern (Rajahmundry, Andhra Pradesh) and central (Jhilmili, Chhindwara) India has shown that the K–T boundary occurs at or near the end of the main phase of Deccan volcanism, demonstrating for the first time a causative relationship between the two events (Keller *et al* 2008, 2009a, b). Keller *et al*'s (2008) biostratigraphic data from the outlying Deccan intertrappean deposits of Rajahmundry area (Andhra Pradesh) on the southeast coast of India, has revealed an early Danian zone P1a assemblages between lower and upper traps of C29R and C29N magnetic polarity zones, respectively (Knight *et al* 2003; Bakshi 2005; Keller *et al* 2008). A similar result was obtained from a recent study of intertrappean deposits at Jhilmili (District Chhindwara, MP) where a planktic foraminifer assemblage of early Danian (P1a) age was reported above the lower Deccan basaltic flow, which correlates with the end of the main phase of Deccan volcanism (e.g., top of the Ambenali Formation) consistent with recent results from Rajahmundry (Jay and Widdowson 2008; Keller *et al* 2008). The discovery of planktic foraminifers in the Jhilmili intertrappeans provides the first definite age evidence in the main Deccan province. The foraminifers were discovered in association with a dominantly freshwater ostracod assemblage, and include *Parasubbotina pseudobulloides*, *Subbotina triloculinooides*, *Praemurica taurica* and *Globigerina (E.) pentagona*. The Jhilmili foraminifer assemblage is typical of the early Danian *P. eugubina* zone P1a, similar to the assemblage recorded at the intertrappean beds of the Rajahmundry quarries (Keller *et al* 2008). Moreover, it allows correlation of this intertrappean sequence to the shallow marine intertrappean sediments in the Rajahmundry quarries where the lower trap of C29R and the upper trap of C29R–C29N transition age (Knight *et al* 2003; Bakshi 2005; Keller *et al* 2008), are considered correlative, respectively, with the Ambenali and Mahabaleshwar Formations of the Western Ghats

(Chenet *et al* 2007; Jay and Widdowson 2008; Self *et al* 2008). It is important to note that the zone P1a spans about 280 ky, immediately above the K–T boundary (Cande and Kent 1991; Gradstein and Ogg 2004). Thus, the Jhilmili and Rajahmundry lower trap basalt flows mark the end of the main Deccan volcanic phase at or near the K–T boundary and the intertrappean sediments as early Danian immediately following the K–T mass extinction. These results are of great significance because they help demonstrate a cause and effect relationship between the K–T extinctions and the Deccan volcanism.

Another important recent development concerns the duration of Deccan volcanic activity and the recognition of three discrete pulses of volcanism (Chenet *et al* 2007; Keller *et al* 2008). The first of these pulses, which occurred between 67 and 68 Ma, was small but significant. This was followed, after a quiescence of 2 to 3 Ma, by the second pulse of volcanism which can be divided into two major pulses, one starting at chron 29R and ending at the K–T boundary, and the second starting in the upper part of chron 29R and ending within chron 29N. It is also becoming increasingly apparent that the Deccan volcanism spanned a much shorter time than previously realized. Recent paleomagnetic data suggest that individual large single eruptive events (SEEs) making up the volcanic pulses probably occurred in a few decades, as reflected in the lack of secular variation in directions recorded in thick sections around Mahabaleshwar (Chenet *et al* 2008).

2.3 Seaway across central India at ~65 Ma

Apart from their age implications, the discovery of planktic foraminifers in Jhilmili has important implications for the K–T paleogeography of the Deccan volcanic province. The occurrence of early Danian planktic foraminifers in predominantly terrestrial intertrappean sediments at Jhilmili clearly shows that marine incursions occurred into central India during the K–T transition. This seaway (figure 2) would likely have been from the west along the Narmada and Tapti rift valleys as Jhilmili is situated almost at the eastern extension of the Tapti rift valley (Keller *et al* 2009a, b). It should be noted that while the idea of a marine seaway was originally proposed over three decades ago mainly on the basis of paleobotanical data (Bande *et al* 1981; Sahni 1983), conclusive evidence in this regard was missing. Sahni (1983) called this seaway the ‘Trans-Deccan Strait’ and postulated that it extended northwards from the Godavari basin. However, the Narmada rift has been considered more likely for this incursion by Keller *et al* (2009b) because marine sequences (Bagh Beds) of

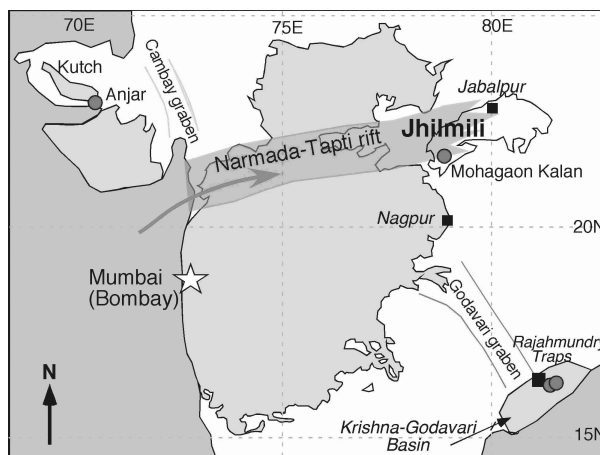


Figure 2. Inferred seaway along the Narmada–Tapti rift in the Deccan volcanic Province, peninsular India (from Keller *et al* 2009b).

Cenomanian–Turonian age have long been known in the Narmada valley, based on ammonites, planktic foraminifera and other groups (e.g., Chiplonkar and Badve 1968; Sharma 1976; Badve and Ghare 1977; Rajshekhar 1996). It is important to note that, prior to the discovery of forams at Jhilmili, evidence for the existence of a seaway during the Maastrichtian was highly controversial and based largely on sedimentological data on the Lameta Formation of central India (e.g., Singh 1981, but see Tandon *et al* 1995 for an opposing viewpoint). Most recently, the Maastrichtian-aged dinosaur-bearing Lameta beds at Jabalpur have been interpreted as lagoonal deposits (Shukla and Srivastava 2008), which supports the existence of a seaway in central India around the K–T transition. The discovery of planktic foraminifers in Jhilmili intertrappeans should be followed by similar finds along the Narmada and Tapti zones. Additional finds of marine microfossils can provide high-resolution age control for the Deccan eruptions and allow correlation of the marine record with the dinosaur-yielding levels within the Deccan Traps.

3. India during collisional phase (~55–45 Ma)

The collision of India with Asia remains one of the most spectacular geological events in the Phanerozoic, and is the best example of continent–continent collision. It has attracted wide attention in recent years with respect to the biota present before and during the collision (Jaeger *et al* 1989; Sahni and Bajpai 1991; Rage and Jaeger 1995; Chatterjee and Scotese 1999; Prasad and Sahni 1999; Briggs 2003; Rage 2003; Sahni 2006; Whatley and Bajpai 2006; Ali and Aitchison 2008; Sahni and Prasad 2008). However, in spite of much research in

a number of geological subdisciplines, some fundamental aspects of the India–Asia collision remain hotly contested. For instance, the exact timing of the initiation of collision has been variously inferred, with estimates ranging from 65 to 35 Ma (e.g., Aitchison *et al* 2007; Ali and Aitchison 2008). However, most workers place the initiation of this event at 55 Ma, and the completion of suturing at ca. 45 Ma, estimates also favoured in this paper. In addition, whereas some workers believe the first continental contact between Asia and India to have occurred in the northwest (e.g., Rowley 1996), others propose that this contact was essentially synchronous all along the Himalaya (e.g., Zhu *et al* 2005).

In India, there is no record yet of continental Paleocene (65–55 Ma) faunas, especially vertebrates, and this has seriously hampered our understanding of India's biotic/physical links during the interval immediately before the collision. The first major biotic events following the Deccan Trap eruptions are recorded in sequences spanning the process of India–Asia collision, from its initiation at ~55 Ma to final suturing at ~45 Ma. These biotic events include the first appearance of modern marine and terrestrial mammal orders in the Indian subcontinent, and they have been documented in recent years from the Eocene sedimentary sequences (~50–54 Ma) in District Surat, Gujarat; Subathu Formation of NW Himalaya in Himachal Pradesh, and the Ghazij Formation of Baluchistan, Pakistan (e.g., Gingerich *et al* 1997, 2001; Bajpai and Gingerich 1998; Bajpai *et al* 2005a; Rose *et al* 2008). Data from the Kutch and Himalayan Eocene have already established the Indian landmass as the centre of origin and early evolution of marine mammals, particularly whales (e.g., Bajpai *et al* 1996; Thewissen *et al* 1996; Bajpai and Gingerich 1998; Bajpai and Thewissen 1998, 2000; Thewissen and Bajpai 2001; Spoor *et al* 2002; Nummela *et al* 2004; Thewissen *et al* 2007). In addition, recent finds of sirenians (sea cows: dugongs and manatees) from the middle Eocene (~45 Ma) of Kutch also point to the importance of Indian sections in uncovering the origin and early evolutionary history of this group of large herbivorous marine mammals (Bajpai *et al* 2006; Bajpai *et al* 2009).

A major recent discovery is the early Eocene (~54 Ma) land mammal fauna in the Cambay Shale deposits at Vastan Lignite Mine, District Surat (Gujarat), western India (e.g., Bajpai *et al* 2005a). The Vastan assemblage represents the oldest known Cenozoic terrestrial mammal fauna from South Asia, and also includes the globally oldest records of a number of modern groups. Prior to this find, the oldest Cenozoic land mammals from South Asia were reported from the

Ghazij Formation (~50 Ma) in a coal mine near Quetta, Pakistan (Gingerich *et al* 1997, 2001; Ginsburg *et al* 1999; Gunnell *et al* 2008). The Vastan area initially yielded fish remains (Samant and Bajpai 2001; Bajpai and Kapur 2006) but thorough prospecting subsequently produced a diverse vertebrate fauna including land mammals that have been described in a series of papers by the IIT Roorkee team (S Bajpai and students/co-workers) and K D Rose and co-workers. Combined together, these investigations show that the Vastan vertebrate fauna comprises amphibians, lizards, snakes, turtles, birds and, most importantly, mammals (Bajpai *et al* 2005a, b; Bajpai *et al* 2006; Bajpai *et al* 2007a, b; Bajpai and Head 2007; Mayr *et al* 2007; Smith *et al* 2007; Bajpai and Kapur 2008; Prasad and Bajpai 2008; Rose *et al* 2008) (Plate 1). Published placental mammal fauna of the Vastan Lignite Mine comprises a number of groups: cambaythere perisodactyls, dichobunid artiodactyls, palaeoryctids, cimolestids, apatemyids, insectivores, adapiform and omomyid primates, chiropterans and lagomorphs. Hyaenodontids and tapiroids also occur (Kapur 2006; Bajpai *et al* 2009). Recently, a major find representing Asia's (possibly also world's) oldest anthropoid primate, named *Anthrasimias*, has come to light (Plate 1f, Bajpai *et al* 2008). As discussed below, the Vastan continental fauna is highly significant from a biogeographic point of view because it comes from a point in time (i.e., near the base of Eocene, ~54 Ma), close to the initiation of the India–Asia collision.

By the middle Eocene (~48 Ma), the Indian subcontinent established subareal contact with the Asian mainland as the intervening Neotethys Sea was in final stages of withdrawal at its northern margin. This led to the establishment of a dispersal corridor between the two landmasses as indicated by the appearance of large mammals of Asian affinity (such as rhinoceroses, brontotheres and tapiroids) in the Subathu Formation of NW Himalaya and correlative Kuldana Formation of Pakistan (see Thewissen *et al* 2001 and references therein). Significantly, the early middle Eocene interval also saw the endemic diversification of certain groups like anthracobunid tethytheres and raoellid artiodactyls, implying partial isolation of the subcontinent by renewed marine incursions (Thewissen *et al* 2001; Clyde *et al* 2003).

3.1 *The Out-of-India hypothesis*

The past few years have seen the emergence of an interesting *Out-of-India* hypothesis which is based primarily on molecular phylogeny and divergence timings of modern biota. This hypothesis holds that several faunal and floral groups in

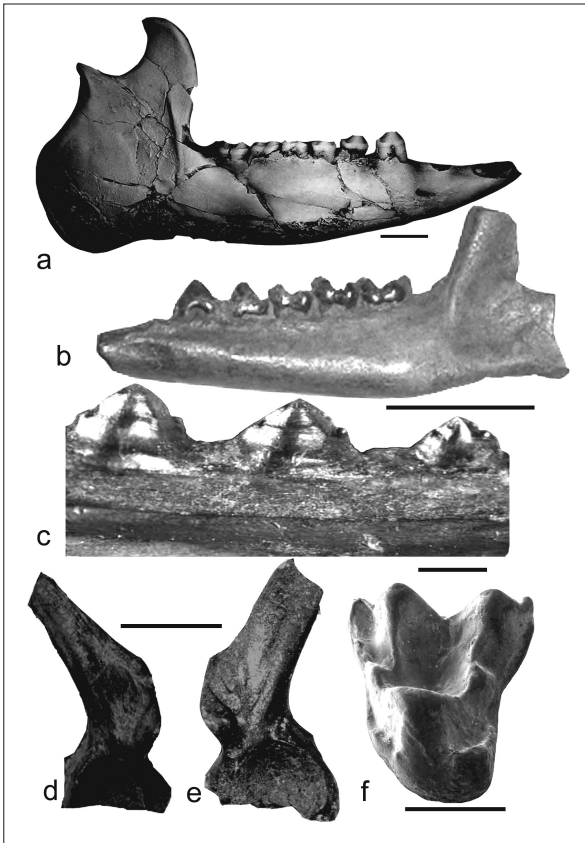


Plate 1. Early Eocene (~54 Ma) vertebrate fossils from Vastan Lignite Mine, Surat, Gujarat. (a) lower jaw of *Camabaytherium* a perissodactyl (scale bar = 1 cm); (b) lower jaw of *Gujaratia*, an artiodactyl (scale bar = 1 cm); (c) jaw of *Tinosaurus*, an agamid lizard (scale bar = 1 mm); (d-e) ilia of ranoid frogs (scale bar = 2 mm); (f) molar of *Anthrasimias*, an anthropoid primate (scale bar = 1 mm).

the modern Asian biota originated in the Indian subcontinent or other Gondwanan landmasses and that these Gondwanan forms were rafted northwards on the drifting Indian plate, eventually spreading to the northern landmasses (Asia, Europe and North America) as a consequence of the early Tertiary India-Asia collision (Karanth 2006). Molecular data supporting this hypothesis comes from diverse modern groups including ranids and caecilians (Amphibia), acrodont lizards, cichlid fishes, ratite birds, and crypteroniaceae plants (e.g., Macey *et al* 2000; Bossuyt and Milinkovitch 2001; Cooper *et al* 2001; Conti *et al* 2002; Bossuyt *et al* 2006).

The Out-of-India hypothesis was originally inspired by the virtually simultaneous appearance of several modern orders of mammals, particularly Artiodactyla (e.g., deer, goats, hippos), Perissodactyla (e.g., horses) and Primates (e.g., humans) across the northern (holarctic) continents near the Paleocene-Eocene boundary at ca. 55 Ma (Krause and Maas 1990). This event is now widely considered to be linked to an extreme global greenhouse

warming event (e.g., Gingerich 2006). Krause and Maas (1990) suggested that the modern mammalian orders together with hyaenodontids, an extinct family of carnivorous mammals, arrived in Asia by rafting on the drifting Indian plate. Study of patterns of this mammalian dispersal (involving migration routes, speed of dispersal, rate of evolution) involves integration of the diverse fields of phylogenetics, biogeography and geochronology (e.g., Bowen *et al* 2002; Hooker and Dashzeveg 2003; Smith *et al* 2006).

Fossil evidence bearing on the Out-of-India dispersal hypothesis is critical but such evidence is currently scarce and limited to only a few faunal and floral groups from the Cretaceous-early Eocene deposits in India. These include the ranoid frogs from both the late Cretaceous and early Eocene (Prasad and Rage 2004; Bajpai and Kapur 2008); agamid lizards from the early Eocene (Prasad and Bajpai 2008); late Cretaceous freshwater ostracods (Whatley and Bajpai 2006); oldest grasses (Prasad *et al* 2005) and the plant *Lagerstroemia* (Lythraceae) (Liu 2008). Intertrappean freshwater ostracod faunas provide interesting insights into the issue of Out-of-India dispersal (Whatley and Bajpai 2006). A number of intertrappean ostracod genera appear to be restricted to India in the Maastrichtian-Danian, becoming subsequently more widely distributed. These include *Paracyprretta*, *Moencypris*, *Centrocypris* and *Pseudocypris*. The widespread genus *Paracyprretta* is typical of the Indian intertrappeans and gives them their unique character. It probably originated in India and subsequently migrated out of India to become diverse, for example, in Africa at the present day (Whatley and Bajpai 2006). Support for an Out-of-India dispersal also comes from the recent discovery of the oldest agamid lizards in the Triassic and early Eocene of India.

Palynofossil records have not yet been evaluated in detail with respect to the Out-of-India dispersal, but preliminary assessment (Prasad and Garg 2008) suggests that several Gondwanan tropical rainforest lineages dispersed to SE Asia after its collision with India.

It is of much current interest to see if the pattern of Out-of-India dispersal is supported by additional taxa among plants, vertebrates and invertebrates. The evidence from vertebrates (tetrapods) is much more convincing in this regard. Ongoing studies on the Vastan fauna are expected to provide significant insights in this regard. Apart from the agamid lizards and ranid frogs, available data on the evolutionary grade of some of the mammalian taxa from Vastan also suggest a possible Indian origin and a subsequent dispersal to holarctic continents as a result of the India-Asia collision. These taxa may possibly include primates,

lagomorphs, artiodactyls and cambaythere perissodactyls. For instance, the two recently described primates from Vastan, *Marcgodinotius* and *Vastanomys*, have been shown to lie, respectively, near the base of the Adapoidea and Omomyoidea, closest relatives (sister groups) of the modern strepsirrhines and haplorrhines (Bajpai *et al* 2005a, 2007b, 2008). As mentioned above, the oldest known anthropoid from Asia has also been described from Vastan (Bajpai *et al* 2008). Also, *Gujaratia*, the new artiodactyl genus named from Vastan (with the type species *Gujaratia pakistanensis*, Bajpai *et al* 2005a) occurs at the base of cetartiodactyls, a clade comprising even-toed ungulate mammals (Geisler and Theodor 2009). Thus, it is possible that the ancestral stocks of these mammalian taxa may have originated in India near the Paleocene-Eocene boundary and moved out when geographic or ecological barriers were removed around the initial India–Asia contact at ca. 55 Ma.

On the other hand, fossil data interpreted to be at variance with the Out-of-India dispersal have been presented by Clyde *et al* (2003), based on their study of the Early Eocene (ca. 50 Ma) Ghazij mammal fauna of Baluchistan (Pakistan). According to Clyde *et al* (2003), the mammal fauna of the Ghazij Formation is relatively endemic in the lower part, while towards the upper part this fauna becomes progressively more cosmopolitan, implying mammalian dispersal *in to* rather than *out of* India. However, the mammal-yielding intervals of the upper Ghazij Formation are distinctly younger than the Cambay Shale of Vastan mine by about 4 million years, or possibly more (Gunnell *et al* 2008; Garg *et al* 2008). Hence, in the event of an *in to* India dispersal, a difference of about 4 m.y. between the first appearance of artiodactyls, perissodactyls and primates (APP) in the Pakistani and Indian sections, strongly suggests that the exchanges between the Indian subcontinent and Asia were spatially varied and may not have been geologically instantaneous. In any case, much of the Ghazij mammal assemblage is yet to be described, hence its precise relationship to the Vastan fauna remains unknown. Furthermore, the available data suggest that the faunal migrations between India and Asia were bidirectional although the exact dispersal routes still need to be worked out. Based on data from the Ghazij Formation, Gingerich *et al* (1997) suggested a northwesterly route, whereas Chatterjee and Scotese (1999) and Ali and Aitchison (2008) proposed that faunal exchanges first occurred *via* the NE corner of the Indian subcontinent, the timing of these latter estimates varying from 50 to 57 Ma. Alternatively, Rana *et al* (2008) favoured a dispersal route from Europe to Asia *via* the Turgai Strait and then to India *via* its leading edge, Hooker

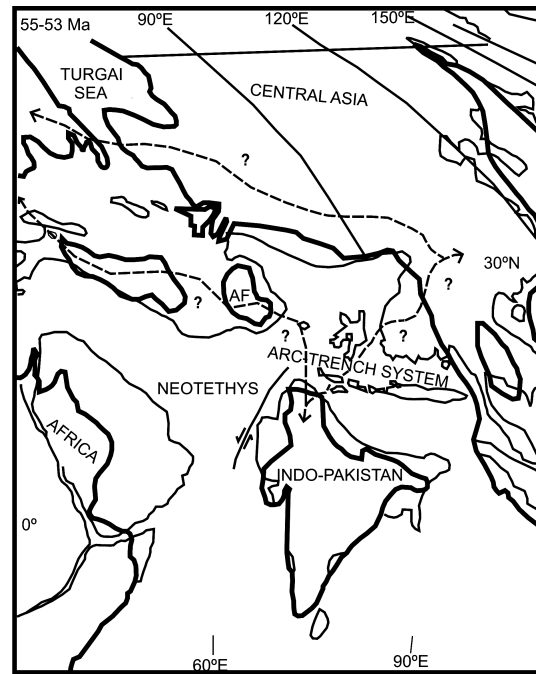


Figure 3. Paleogeographic setting of the Indian subcontinent around 54 Ma. Dashed lines indicate possible dispersal routes for faunal exchanges (modified after Gingerich *et al* 1997).

and Dashzeveg (2003) also favoured multiple land mammal dispersal across the Turgai Straits from Asia to Europe during low sea levels in the late Paleocene and early Eocene. Some of the possible dispersal routes are shown in figure 3.

Summing up, the available fossil record of diverse faunal and floral groups does provide limited support for the Out-of-India hypothesis. However, except in a few cases, the biogeographic significance of these taxa is yet to be evaluated in a rigorous phylogenetic context based on more complete fossil material.

4. Conclusions

Paleontological investigations carried out during the past decade have provided new insights into India's biotic evolution in a geodynamic context during the period from Deccan volcanism (65 Ma) until the India–Asia collision (55–45 Ma). The main advances can be summarized as follows:

- The discovery of early Paleocene (P1a) planktic foraminifers in a Deccan intertrappean section at Jhilmili, District Chhindwara (Madhya Pradesh), in central India is of considerable significance as it indicates that the K–T boundary coincided with the end of the main phase of Deccan volcanism, similar to recent results from sections near Rajahmundry (Keller *et al* 2008, 2009a, b). These results imply that the Deccan

continental flood basalt eruptions were a major contributor to the mass extinctions.

- Recent data indicate three Deccan volcanic pulses with phase-1 at 67.5 Ma followed by a 2 m.y. period of quiescence. Phase-2 marks the main Deccan volcanic eruptions in Chron 29R near the end of the Cretaceous and accounts for ~80% of the entire Deccan lava pile. The final phase-3 is relatively minor, coincides with the early Danian Chron 29 R/Chron 29 N transition and also witnessed several of the longest lava flows (Chenet *et al* 2007; Keller *et al* 2008).
- The discovery of planktic foraminifers in the main part of the Deccan province indicates that a seaway existed in central India during the Cretaceous-Tertiary (K-T) transition around 65 Ma. These marine incursions probably followed the Narmada and Tapti rift zones where a seaway is already known to have existed during the Cenomanian-Turonian (Bagh Beds). Along the proposed seaway along the Narmada, a rich and diverse fauna of dinosaurs and associated vertebrates flourished during the Maastrichtian. Their diversity decline and eventual extinction may now be evaluated within the context of this major trans-India seaway and the killing effects of the main phase of Deccan volcanism near the end of the Cretaceous (Keller *et al* 2009a, b).
- Extensive endemism among the freshwater ostracods from the Deccan intertrappean deposits, based on the recognition of over 75 new species, suggests India's geographic isolation around 65 Ma (Whatley and Bajpai 2006), consistent with the traditional geophysical data. The co-existence of Laurasian elements in the Deccan intertrappeans is better explained in terms of transoceanic (sweepstakes) dispersal rather than the previously proposed terrestrial contact between India and Asia near the K-T boundary. However, the common presence of Gondwanan elements (e.g., abelisaurid dinosaurs) in the late Cretaceous of India, Madagascar and South America is most consistent with physical links between these landmasses until about 80 Ma or, somewhat earlier in the Cretaceous.
- Near the Paleocene-Eocene boundary (~54 Ma), broadly coincident with the initiation of India-Asia collision, primitive members of at least 10 modern land mammal orders appear abruptly in the Indian fossil record, at a coal mine at Vastan near Surat, western India (e.g., Bajpai *et al* 2005a, 2006, 2007a, 2008; Rose *et al* 2008). This globally significant fauna includes perissodactyls (e.g., horses), artiodactyls (e.g., deer), primates (e.g., humans), insectivores, bats and lagomorphs and several other groups. The Vastan mammal assemblage possibly dates the earliest Cenozoic faunal exchanges between India and

Asia, and raises the possibility of an Indian origin and subsequent migration to northern continents for some of the major groups. A similar Out-of-India dispersal as a consequence of India-Asia collision is supported by the fossil record of diverse taxa such as freshwater ostracods, ranid frogs, agamid lizards, grasses, diatoms and most importantly, whales (Bajpai and Gingerich 1998; Thewissen *et al* 2007).

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