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HISTORICAL BIOGEOGRAPHY OF THE LATE CRETACEOUS VERTEBRATES OF INDIA: COMPARISON OF GEOPHYSICAL AND PALEONTOLOGICAL DATA

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Abstract—The Cretaceous was a special time for the Indian plate as it was separated from Gondwana landmasses and started its northward journey across the Tethys Sea towards the Equator. The northward movement of this plate implied shifting latitudes and climate belts, until it finally collided with Asia during the early Cenozoic. Geophysical data and plate tectonic models show that after splitting from Gondwana, the Indian plate remained as an isolated continent for more than 45 Ma during the Cretaceous; thus, it predicts a remarkable biotic endemism for the continent. Paleontological data on the Cretaceous vertebrates of India is best known for Maastrichtian time; in turn, the pre-Maastrichtian record is very poor—it contains very few fossils of fishes and marine reptiles. The Maastrichtian fossil record comprises vertebrates of Gondwana and Laurasian affinities and some endemic, ancient lineages as well. In order to explain the presence of vertebrates of multiple affinities in the Late Cretaceous of India, various biogeographic models have been proposed. The latter include extinctions, endemism, vicariance, dispersal (sweepstakes, filters and corridors), "Noah's Ark," "Docked Noah's Ark," "Viking Funeral Ship" and "land spans," thus accounting for the biotic implications of the Cretaceous northward drifting of the Indian plate. The current paleontological data suggest the existence of both southern and northern biotic dispersals/connections, however, geophysical data instead favor a biotic endemism for the Indian plate during the Late Cretaceous. Here, an attempt has been made to document the consistencies between geophysical and paleontological data, in order to understand the biogeography of the Late Cretaceous vertebrates of India.

INTRODUCTION

Reconstruction of historical biogeographic models and patterns has always been a major challenge for paleontologists. The rise of the plate tectonic theory in the early 1960's revolutionized their thinking, while providing a new framework for understanding the biogeography of the past. The theory of plate tectonics states that the rigid lithosphere of the earth is divided into a number of variable-sized plates that move independently in relation to one another due to magmatic convection currents within the asthenosphere of the earth's mantle (Stanley, 2009). The movement of these plates is variable, with some of them moving faster than others, and has significantly altered the geologic and biologic history of the earth through the ages.

Three major plate boundaries are recognized: divergent, where plates move apart from each other, and form mid-oceanic ridges and rift valleys; an example of this is the Mid-Atlantic Ridge or the East African Rift Valley. The second type of plate boundary is the convergent one, where plates come together or collide with each other and form volcanic island arcs, oceanic trenches, and mountain chains; an outstanding example of this are the Himalayas. Finally, in the transform boundary, the plates slide laterally past one another (Wicander and Monore, 2010). These plate boundaries can occur along continental margins, within continents or within oceans (Lieberman, 2000). Various biogeographic models have been associated with specific types of tectonic movement of plates, as extinctions, endemism, vicariance, or dispersal (e.g., Briggs, 1987; Crisci, 2001).

Historically, the divergent and convergent types play an important role in shaping the biogeographic patterns of continents: they are directly involved in the creation of new, or the closing of, oceanic barriers, by breaking previously contiguous landmasses, or docking separated landmasses, respectively (Briggs, 1987). Both types were decisively involved in the Cretaceous-Cenozoic paleogeographic history of the Indian plate.

The rise and fall of sea level is also considered another event closely related to plate tectonics and climate changes that can profoundly affect biogeographic patterns. As the global temperature drops, the sea level falls and exposes once submerged terrains, which serve as corridors and thus allow terrestrial faunas to expand their range from one landmass to another. On the other hand, rise of sea level creates new oceanic barriers and fosters the isolation in the terrestrial biota, but has adverse effects on the marine biota.

India provides a unique model for evolutionary studies: (1) it is a very large landmass that broke apart from one supercontinent; (2) it stays isolated for a long time-lapse until it met another supercontinent; (3) its northeastern drift towards southern Asia consisted in a trans-Equatorial, trans-Hemispherical migration, which happened quite rapidly in geologic terms; and finally, (4) it captures the departure from one type of biota (that of Jurassic Gondwana) to another, dramatically different one (Cenozoic Laurasia). Probably, no other landmass provides such a complex mixture of paleogeographic, paleobiogeographic, and evolutionary scenarios.

A number of historical biogeographic approaches have been suggested to explain the Late Cretaceous terrestrial biota of the northward drifting Indian plate (see e.g., Sahni and Khosla 1994a-c; Krause et al., 1997; Sahni et al., 1999; Khosla and Sahni, 2000; Khosla, 2001, 2014, 2015; Prasad and Sahni, 1999; Chatterjee and Scotese, 2010; Sahni, 2010; Prasad, 2012; Verma et al., 2012a; Bajpai et al., 2013; Chatterjee et al., 2013; Khosla and Verma, 2015; Verma, 2015). In turn, a wealth of geophysical and paleontological data has been generated in the last 40 years to better document the tectonic evolution of the Indian plate and associated historical biogeographic patterns (Prasad and Sahni, 1988; Krause et al., 1997; Gaffney et al., 2001; Hay et al., 1999; Prasad et al., 2007a, 2010, 2013; Ali and Aitchison, 2008; Chatterjee et al., 2013; Goswami et al., 2013). A recently discovered, surprising terrestrial biota from the Late Cretaceous of India suggests a more complex Late Cretaceous biogeography than plate reconstructions alone would predict (e.g., Khosla and Verma, 2015). Hence, the geophysical data does not fully complement the paleontological data and vice versa, as far as the historical biogeography of the Late Cretaceous biota of India is concerned.

This communication has two main objectives. The first is to review the geophysical and paleontological data that document the tectonic and biogeographic history of the Indian subcontinent. The second objective is to find discrepancies or biases in these data, in order to understand why the former fail to complement the latter.

BIOGEOGRAPHY AND BIOGEOGRAPHIC MODELS

Biogeography analyzes the geographic distribution of organisms in relation to space and time and helps in the understanding of the relationships between the evolution of the earth and its biota. The main aim of biogeography is to document how and why living organisms are distributed over the present surface of the earth. In turn, historical (paleo)biogeography attempts to reconstruct distribution patterns of extinct organisms or populations (Rosen,1988; Lieberman, 2000). In a classical paper entitled "Sweepstakes, filters, corridors, "Noah's Arks," and beached viking funeral ships in palaeogeography," McKenna

(1973) made an attempt to bring the usefulness of pre-plate tectonic biogeographic models based on a stable earth system into the context of well-accepted plate tectonic models (cf. Jacobs et al., 2011). He (McKenna, 1973) also emphasized that the three types of faunal links, such as sweepstakes, filters, and corridors proposed by Matthew (1939) and Simpson (1940) are still relevant in the context of moving continents and plate tectonics.

The sweepstakes routes involve faunal interchanges between isolated areas that are difficult to access, and are likely to be used by only few organisms as these are random, unpredictable and of very low success—oceanic rafting is cited as an example of this type of route. Filters consist of those routes that allow dispersal through a limited variety of habitats; only the species that adapt to the environmental conditions of the route are able to pass through it, whereas corridors are those in which almost all organisms are able to cross through. In addition, McKenna (1973) added two more biogeographic types of biotic interchange: "Noah's Arks" and "Beached Viking Funeral Ships." The former are defined as the portions of continental crust that rift apart from their continent of origin along with its biota. These "Noah's Arks," which develop due to the rifting of a continent, first fuel the isolation of the biota, and later may "dock" with a new continent and transfer their biota into the new area (Meert, 2012). "Beached Viking Funeral Ships" are also portions of continental crust that rifted from one landmass, and may later collide and join with new continental areas and introduce the carried fossil biota (extinct in the original area) to the new continent, where the transported biota had never been known previously. "Noah's Arks" are the tectonic features associated with divergent plate boundaries; in turn, "Docked Noah's Arks" and "Beached Viking Funeral Ships" are features associated with convergent plate boundaries (Jacobs et al., 2011; Meert, 2012).

Many other mechanisms, such as extinction, endemism and vicariance, also play an important role in shaping the geographic distribution of organisms. Extinction involves the permanent loss of the species; it happens when the preferred habitat of a species and its adaptation capabilities shrink due to a changing environment. Endemism occurs when a group of organisms is restricted to a particular geographical area; for example, Australasian kangaroos (Diprotodontia). Vicariance models are associated with continental fragmentation: ancestral taxa with a widespread distribution before fragmentation of a landmass, give way to a divergence of lineages of the ancestral stock, with a disjunct distribution, after such a fragmentation (Lieberman, 2000).

While describing the paleogeography of the Caribbean fauna, Iturralde-Vinent and MacPhee (1999) introduced the concept of "landspan" in historical biogeography: "a sub-aerial connection (whether continuous or punctuated by short water gaps) between a continent and an off-shelf island (or island arc)." Recently, Jacobs et al. (2011) presented an account of the possible series of land spans between the Gondwanan subcontinents that may have facilitated the dispersal of faunas prior to their significant fragmentation, which was attained due to the opening of the Atlantic, Pacific and Indian oceans as well as continuing drift and sea-level changes.

The breakup of continents, formation of islands, re-assembly of continents and islands, opening and closing of sea and ocean basins, eustatic changes and climate changes, all strongly influence the development of distinct biogeographic patterns. The breakup of Gondwana continents and dispersal of their constituent biota has provided an ideal natural laboratory to test various biogeographic models associated with the tectonic movement of continents (e.g., Jacobs et al., 2011; Chatterjee et al., 2013). The Indian plate is outstanding in that it fits multiple biogeographic models at different times. For instance, it has been proposed that the Late Cretaceous Indo-Madagascar block served as a "Noak's Ark" after its separation from Australo-Antarctica. Viewed retrospectively, the Indian subcontinent may have functioned as a "Beached Viking Funeral Ship" after its separation from Madagascar. Finally, it could represent a case of "Docked Noak's Ark" by the time of the India/Asia collision (Jacobs et al., 2011; Meert, 2012).

INDIA FROM GONDWANA TO ASIA: A GEOPHYSICAL PERSPECTIVE

The plate tectonic theory is largely based on geophysical data derived from paleomagnetism, linear magnetic anomalies, apparent polar wander curves and structure or tectonics. However, data collected from other sources like deep sea drilling projects, ocean drilling programs, stratigraphy, sedimentology, paleontology, paleogeography, bathymetry, geochronology and paleoclimate are also used to reconstruct the tectonic history of continents. Here we bring together geophysical and other data from a range of published sources to provide an account on the current-state-of-knowledge concerning the separation and dispersal of the Indian plate from Gondwana up to its collision with Asia during the late Mesozoic to early Cenozoic. The tectonic story of the Indian subcontinent began with the starting of rift of the Gondwana supercontinent and ended with its collision with Asia. In the early 1910s, Alfred Wegener, a German meteorologist, presented the view that all the modern continents of the earth were, by the late Paleozoic, united and forming a single megacontinent, which he named "Pangaea" (which means "all lands;" Wegener, 1915). Pangaea was encircled by the continuous stretch of a superocean, "Panthalassa" (a term meaning "all oceans") from the late Paleozoic to the Triassic (Howarth, 1981). During the early Mesozoic, Pangaea started to split into two supercontinents: "Laurasia" (term that refers to a combination of Laurentia, a region of Canada, and Asia) to the north and "Gondwana" (name derived from the land of the Gonds, an ancient tribe of central India) to the south; both supercontinents were partially separated by a wedge-shaped sea known as the "Tethys Sea" (Hallam, 1981; Hocutt, 1987; Fig. 1). The concept, extension and progress of these landmasses are widely accepted in the context of plate tectonic dynamics (e.g., Dietz and Holden, 1970).

It has been proposed that the rifting and subsequent drifting of continents are features commonly characterized by the development of a series of deep-seated mantle plumes and sea-floor spreading processes; actually, the Gondwana fragmentation constitutes an excellent natural laboratory where the mantle plume model can be tested (Storey, 1995; Steven and Stegman, 2011). In addition, continental split is in many cases associated with the eruption of widespread flood-basalt provinces; thus, the dating of such basaltic provinces provides approximate dates for the splitting processes. Notwithstanding, it is still a matter of debate whether rifting and subsequent drifting above the mantle plumes was a mechanism for the breakup of Pangaea (e.g., Scotese, 1991; Jokat et al., 2003).

The supercontinent Gondwana comprised all past (post-Paleozoic) southern continents—South America, Africa, Antarctica, Australia, India, Madagascar—as well as a number of micro-continents, for example, the Seychelles, began to disintegrate from its northern sister Laurasia during the onset of the breakup of Pangaea about 215 Ma ago (Dietz and Holden, 1970; Scotese et al., 1988; McLoughlin, 2001). After its separation from Pangaea, Gondwana remained intact as a single entity for about another 50 Ma (Cracraft, 1974; Scotese, 1991, 2001; Jokat et al., 2003). Indeed, the sequential breakup and rifting of Gondwana that created the modern southern oceans initiated during the late Early Jurassic (ca. 180 Ma), a time marked by the beginning of the initial separation between East and West Gondwana (Storey, 1995; Jokat et al., 2003).

It is a well established fact that the initial East and West Gondwana separation started in the north, progressed southwards and was associated with the emplacement of mantle plume-related flood basalts

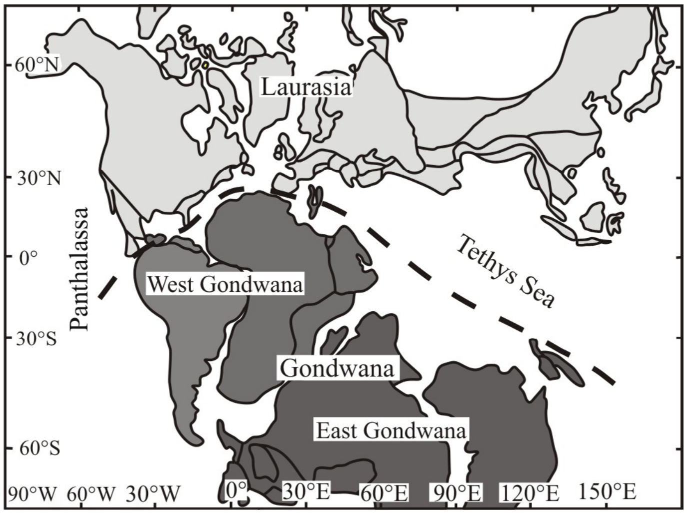


FIGURE 1. Paleogeographic map showing the megacontinent, Pangea, during the Jurassic Period, with Laurasia in the north and Gondwana in the south. Modified after Smith (1992).

in the Karoo Province, southern Africa, dated at ca. 182 Ma, and Ferrar Province in the Trans-Antarctic Mountains, East Antarctica, by 176 Ma (Simpson et al., 1979; Storey, 1996). Shortly after the initial intra-continental rifting among Gondwana, both the East and West Gondwana blocks started rifting (ca. 165 Ma); this led to the formation of a seaway by the initiation of sea-floor spreading in the Somali, Mozambique, and, possibly, the Weddell Sea basins (Coffin and Rabinowitz, 1987; Storey, 1995; Ségoufin et al., 2004). This spreading phase continued until ca. 116 Ma (Schettino and Scotese, 2005; Ali and Aitchison, 2008); most of this time, eastern Africa and western Madagascar remained close to each other, thus suggesting that numerous biotic interchanges may have occurred among these blocks (e.g., Ali and Aitchison, 2008).

Rifting in West Gondwana between South America and Africa probably started in the Early Cretaceous (ca. 135 Ma ago), marked by the initial opening of the South Atlantic Ocean (Barker et al., 1991; Grunow et al., 1991; Torsvik et al., 2009). It is believed that the emplacement of the Paraná in Brazil (South America) and Etendeka in Namibia (Africa) flood basalts, dated at ca. 137-127 Ma, were linked to the initiation of the split between South America and Africa (Renne et al., 1992; Turner et al., 1994; Storey, 1995; McLoughlin, 2001). Studies show that the rifting of these two continents was not synchronous, as the earliest oceanic crust was formed in the south of the South Atlantic Ocean and the final physical separation did not occur until the Aptian-Albian boundary (Binks and Fairhead, 1992; Barron, 1987; Torsvik et al., 2009). As a consequence, the continental margins of northern South America and Africa remained connected until 119-105 Ma along the Guinea Fracture Zone (e.g., Binks and Fairhead, 1992; McLoughlin, 2001) and by two seamounts, the Walvis Ridge and Rio Grande Rise, until 100-90 Ma (Scotese, 2001; Sereno et al., 2004). It is well accepted that before the Cenozoic, southernmost South America and the northern tip of Western Antarctica remained physically connected, and that the earliest separation may have occurred in the Powell Basin area ca. 50 Ma (Lawver and Gahagan, 1998; Reguero et al., 2013). Southern Africa separated from Antarctica by140-122 Ma, a time lapse marked by the emplacement of the Mozambique Ridge (König and Jokat, 2010).

For much of the Mesozoic, India resided in the Southern Hemisphere as a part of East Gondwana (also including Antarctica, Australia, Madagascar, and the Seychelles). Adjacent landmasses included Africa, Madagascar and Seychelles to the west; Sri Lanka and Antarctica to the south; Australia to the northeast, and the Neo-Tethys Sea occupied its entire northwestern to northeastern margins (Scotese, 1991; Smith et al., 1994; Storey, 1996; Ali and Aitchison, 2008; Chatterjee et al., 2013; Fig. 2). The chronology of the tectonic history of the Indian subcontinent has been variously documented (e.g., Rabinowitz et al., 1983; Powell et al., 1988; Storey, 1996; Hay et al., 1999; Briggs, 2003; Chatterjee and Scotese, 1999; Ali and Aitchison, 2008; Chatterjee et al., 2013; Gibbons et al., 2013; Figs. 3-4).

India began to disperse first from Africa during the Middle Jurassic (ca. 165-150 Ma), when there was initial rifting between East Gondwana and West Gondwana that led to formation of the Somali Basin, which in turn indicates the beginning of the West Indian Ocean (Rabinowitz et al., 1983; Storey, 1996; Chatterjee et al., 2013). During the mid-Early Cretaceous (ca. 130-120 Ma ago), the Indo-Madagascar block began to separate from Antarctica-Australia; this led to the formation of the East Indian Ocean (Powell et al., 1988; Chand et al., 2001). It is well documented that this separation was associated with the emplacement of extensive magmatism, the Rajmahal-Sylhet basalts, Bunbury basalts and Kerguelen Island basalts caused by the Rajmahal-Kerguelen mantle plumes.

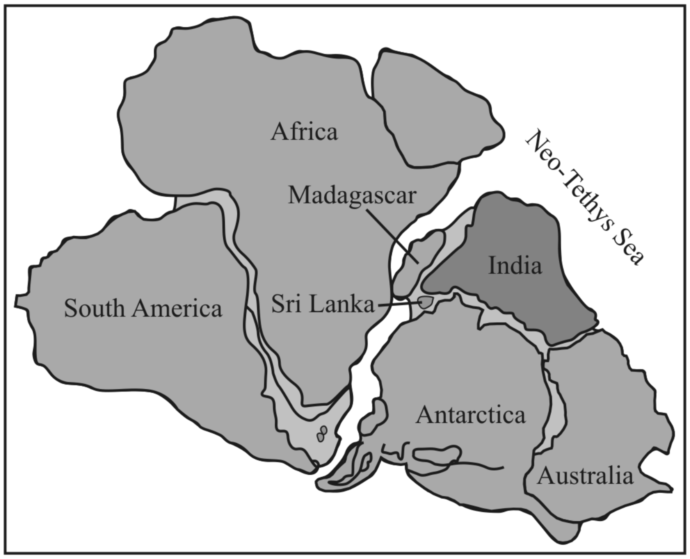


FIGURE 2. Paleogeographic map of Gondwana showing the position of India relative to other plates at 160 Ma. Modified after Storey (1995).

The Kerguelen Plateau basalts (118-115 Ma) are an oceanic plateau that lie between India and Antarctica after their separation (Storey, 1995). Hay et al. (1999) suggested that a large portion of the Kerguelen Plateau was sub-aerially exposed during the Late Cretaceous, which indirectly connected Indo-Madagascar to South America via Antarctica as late as 80 Ma (Fig. 3I). Case (2002) argued that Antarctica and Madagascar were linked by the Gunnerus Ridge during the mid-Late Cretaceous. In contrast, Ali and Aitchison (2009), on the basis of geophysical modeling, proposed that a large portion of the Kerguelen Plateau was sub-aerially exposed until the Early-Late Cretaceous boundary ca. 95-90 Ma ago, being exposed only as a small portion of the plateau; its margins were covered by deep-sea waters ,and hence, it never served as a land connection between Antarctica and Indo-Madagascar during the Late Cretaceous. Following this, Ali and Krause (2011) refuted Case's hypothesis; instead, they proposed that southern Madagascar and the Gunnerus Ridge of eastern Antarctica were also separated by a wide marine gap in the Late Cretaceous.

The India-Seychelles block separated and drifted away from its sister-continent, Madagascar, around 88 Ma; this occurred concomitant with the opening of the Mascarene Basin, an event linked to the Marion mantle plume (Storey et al., 1995; Torsvik et al., 2000). While crossing over the Réunion mantle plumes, Seychelles dismembered from India by the Cretaceous-Paleocene boundary (66 Ma). Finally, India collided with Asia by 50 to 55 Ma (latest Paleocene-early Eocene), leaving evidence of drifting in the forms of the Ninetyeast Rigde, Réunion Island and Mascarene-Chagos-Laccadive Ridges in the Indian Ocean (Patriat and Achache, 1984; Hooper, 1990; Storey, 1995; Ali and Aitchison, 2008; Chatterjee et al., 2013). The force of the India/Asia collision produced the world's youngest and highest fold mountain system on the earth: the Himalayas and the Tibetan Plateau, a plateau of such extent and height that it altered global climate, including creation of the unique monsoon systems for the Indian subcontinent (Chatterjee et al., 2013).

PREDICTIONS OF THE GEOPHYSICAL DATA FOR THE INDIAN PLATE

Geophysical data and most of the paleogeographic reconstructions of Gondwana continents indicate that, after separating from other Gondwanan landmasses ca. 135 Ma, particularly from Antarcto-Australia, the Indo-Madagascar block began its long northward journey towards Eurasia. This displacement reached a record speed of 18-20 cm/year by 90 Ma in the Tethys Sea at the time of the fragmentation of India and Madagascar, slowing down to about 5 cm/year after colliding with Asia by 50 Ma (Johnson et al., 1980; Powell et al., 1988; Storey et al., 1995; Kumar et al., 2007). The Indian plate also witnessed extensive continental flood basalts, i.e., the Deccan volcanic province by the end of the Cretaceous, while crossing over the Réunion mantle plumes and rifting from the Seychelles prior to its collision with Asia (Chatterjee et al., 2013). As per the geophysical data, the Indo-Madagascar block and the Indian plate remained physically isolated up to 45 Ma after its fragmentation from Antarcto-Australia and Madagascar, respectively, during the Cretaceous. In addition to these lengthy periods of continental isolation, the Indian plate suffered a shifting of latitudinal and climatic belts: from tropical arid-temperate to equatorial rainy-subtropical, during the Early to the Late Cretaceous (Chatterjee et al., 2013).

It is interesting to note that if the Cretaceous northward journey of the Indian plate had occurred in this long and extended period of physical isolation with shifting latitudes, climatic belts and concurrent periodic eruptions of the Deccan volcanism by the Cretaceous-Paleocene transition, these factors would have been expected to provide peculiar environmental conditions and sufficient time to develop a highly endemic fauna, as is the case of the Cenozoic biota of Africa, Australia and Madagascar. A summary of the geophysical data and plate tectonics prediction for the on board biota of the Indian plate as well as current status of its fossil record is given in Figure 5.

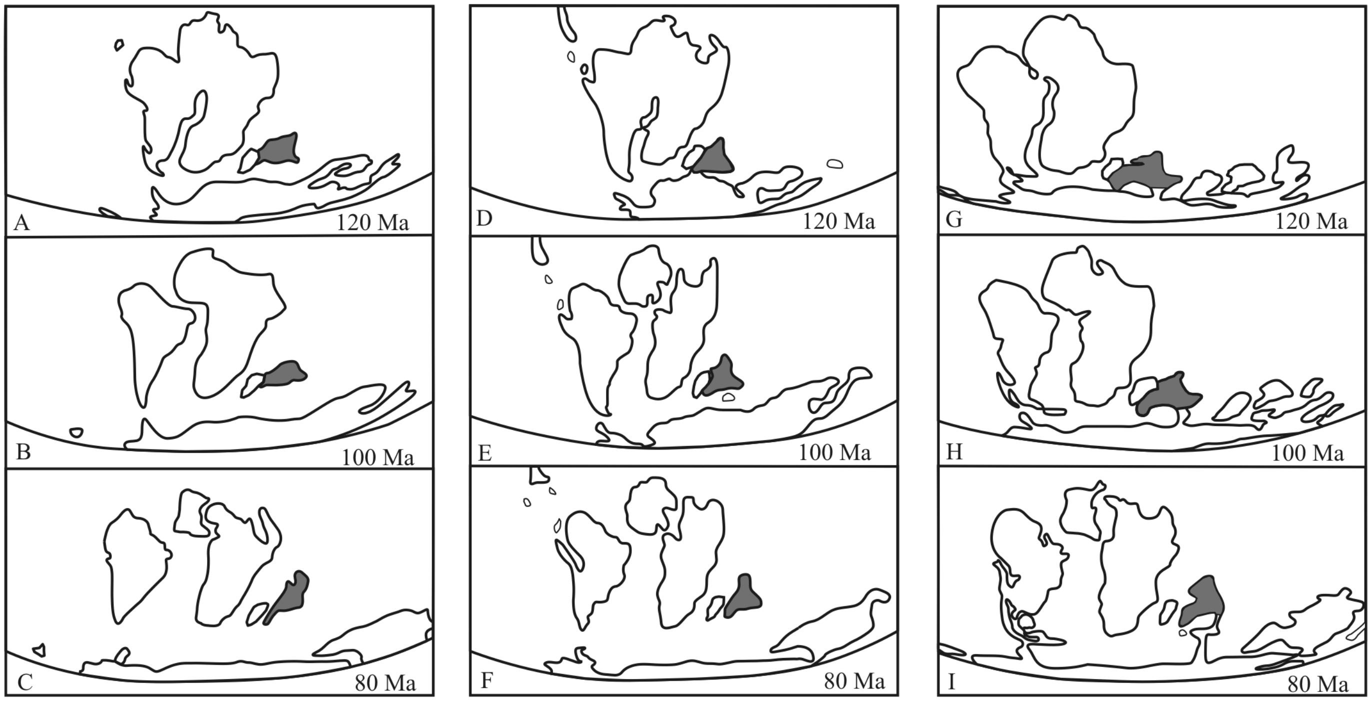


FIGURE 3. Paleogeographic reconstructions of Gondwana landmasses at 120 (**A**, **D** and **G**), 100 (**B**, **E** and **H**) and 80 (**C**, **F** and **I**) Ma showing the relative positions of the Indian plate. A-C after Smith et al. (1994), D-F after Scotese (1998) and G-I after Hay et al. (1999). Maps redrawn and modified after Krause (2003).

ON BOARD CRETACEOUS VERTEBRATES OF INDIA: A PALEONTOLOGICAL PERSPECTIVE

India has vast tracts of Cretaceous deposits that occur both in the peninsular and extra-peninsular regions of India. However, the stratigraphic record of the vertebrate fossils has been discovered from a very few stages of the period from the peninsular region (e.g., Tripathi et al., 2013; Khosla and Verma, 2015; Verma, 2015). It should be noted that the fossil record of vertebrates in India is yet to be documented for most of the Early Cretaceous.

Berriasian to early Albian Vertebrate Record

Vertebrate fossils are poorly documented from the Berriasian to lower Albian deposits of India. Misra and Saxena (1964) described the teleostan fish, *Jhingrania roonwali* Misra and Saxena, 1964, based on a single skeleton, which was recovered from the Barremian-Aptian freshwater sediments of the Rajmahal Formation, Jharkhand. A few fish remains of teleosts represented by scales, vertebrae, teeth and fragmentary to a few complete skeletons, and a single shark tooth, were reported from the marginal marine Raghavapuram Mudstone (Barremian to early Albian), East Coastal Gondwana, West Godavari District, Andhra Pradesh (Baksi, 1973). In addition, Baksi (1973) identified the skeletal material as *Clupavus* cf. *neocomiensis*, which was previously known from the Berriasian to Cenomanian deposits of Morocco; he concluded that *Jhingrania roonwali* seems to have a close affinity with it. Prasad et al. (2004) described additional fish remains, comprising teeth and scales of an actinopterygian from the freshwater Neocomian Gangapur Formation, Pranhita-Godavari valley, Telangana. Finally, a marine plesiosaur reptile, *Thaumatosaurus indicus* Lydekker, 1889, was reported from the upper Tithonian to Albian shallow marine Umia Formation of the Kachchh Basin, Gujarat (Verma et al., 1977).

Latest Albian to Coniacian Vertebrate Record

The fossil record of vertebrates from the latest Albian to Coniacian mainly comes from the shallow marine deposits of the Cauvery and Narmada basins of southern and central India, respectively. The shark fauna includes *Squalicorax* (Anacoracidae), *Dwardius* and *Cretalamna* (Otodontidae), ?*Eostriatolamia* sp. (Odontaspididae), *Protosqualus* sp. (Squalidae), *Gladioserratus* and ?*Notidanodon* (Hexanchidae), *Cretodus* (Lamniformes) and *Ptychodus* (Ptychodontidae). They were reported from the Cenomanian to Turonian deposits of the Uttattur Group of the Cauvery Basin (Underwood et al., 2011; Verma et al., 2012b; Verma, 2015). Earlier, Egerton (1845) described some sharks and pycnodonts from the Late Cretaceous sediments of the Cauvery Basin, exposed around the Pondicherry area. Stoliczka (1873) documented the presence of pycnodont (?*Pycnodus* sp.) fish from the Uttattur Group. Lydekker (1879) and Underwood et al. (2011) described some fragmentary material of the marine ichthyosaur reptile, *Platypterygius indicus* Lydekker, 1879, from the latest Albian to Turonian deposits of the Uttattur Group. A plesiosaur, *Dravidosaurus blanfordi* (Yadagiri and Ayyasami, 1979), was documented from the Coniacian deposits of the Trichinopoly Group of the Cauvery Basin (Yadagiri and Ayyasami, 1979; Verma, 2015). However, the ptychodont, *Ptychodus*, and a few, indeterminate lamniform sharks, were also reported from the Cenomanian to Turonian sediments of the Bagh Formation (Verma, 1965; Chiplonkar and Ghare, 1977).

These fish faunas have close resemblance with those known from the Cauvery Basin, and some inter-dispersal has been proposed between the Cauvery and Narmada basins during latest Albian to Turonian time (e.g., Verma, 2015). The report of a titanosaur sauropod dinosaur from the Cenomanian-Turonian deposits of the Bagh Formation, Narmada Basin by Khosla et al. (2003) extended the record of the group back by more than 30 Ma in India. It has been observed that both the age and lithology of the dinosaur-yielding sediments of the Bagh Formation are very much similar to those of the Bahariya Formation of Egypt (Smith et al., 2001). Although the sauropod material still awaits a finer taxonomic assignment, it is considered to have close affinities with *Saltasaurus*, a titanosaur from the Late Cretaceous of Argentina (Khosla et al., 2003; Sahni, 2010). Due to its fragmentary nature, the pre-Maastrichtian vertebrate fossil record has received little attention for understanding the Cretaceous biogeography of India.

Maastrichtian Vertebrate Record

The Maastrichtian record is the most intensively sampled interval in India, which comes mainly from sediments associated with the Deccan volcanic province in peninsular India; this record is important in the understanding of various biogeographic patterns associated with the drifting Indian plate (e.g., Khosla and Verma, 2015 and references therein). Recently, vertebrate fossils have also been documented from the Maastrichtian sediments of the Kallamedu Formation in the Cauvery Basin, Tamil Nadu, and of the Mahadek Formation, Khasi Group, Meghalaya. Fishes are dominant in the recovered Maastrichtian faunas of the Deccan volcanic province, and have been referred to various groups of chondrichthyans (Dasyatidae, Orthacodontidae, Myliobatidae, Rhombodontidae and Rajiformes) as well as osteichthyans such as Semionotiformes, Lepisosteiformes,

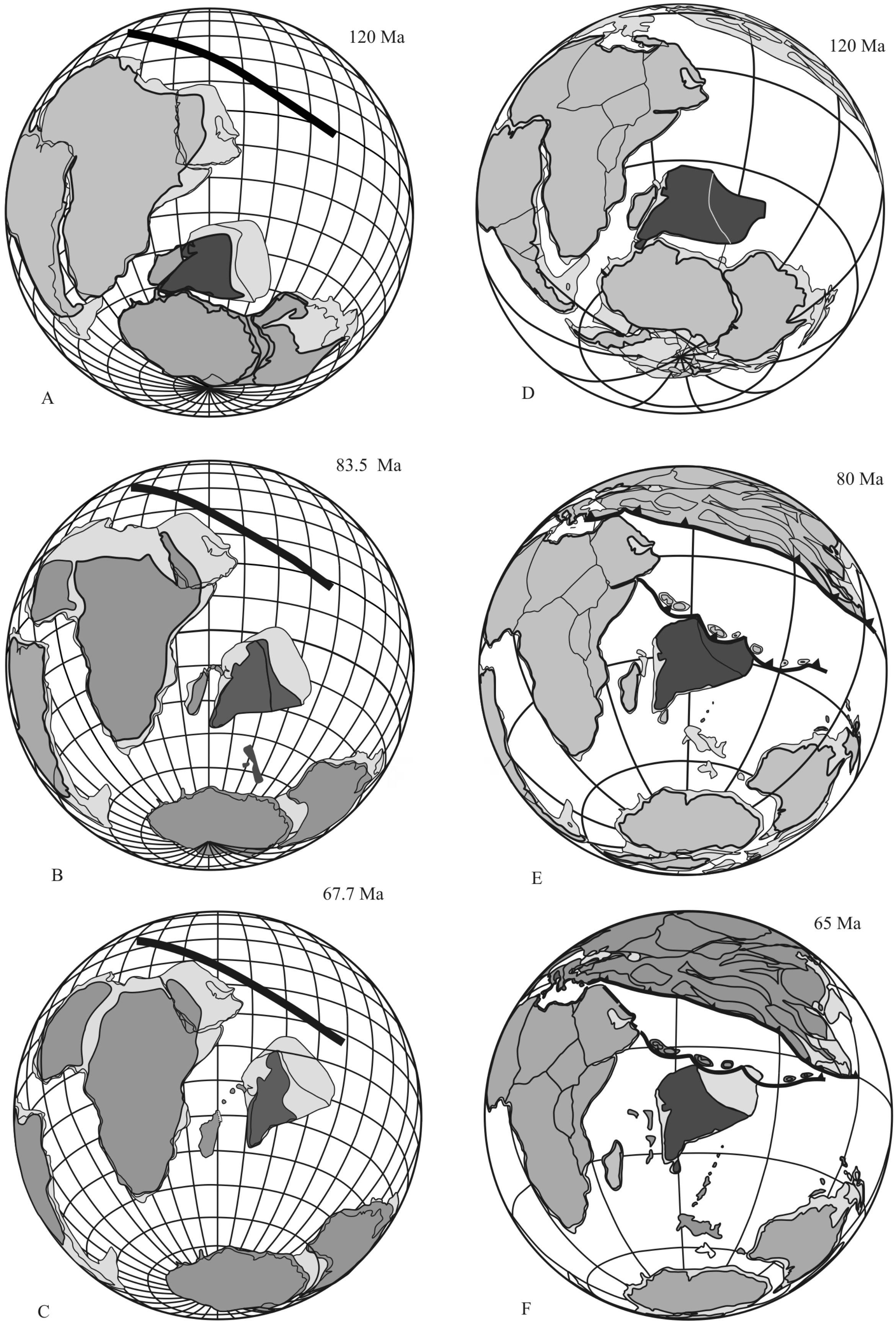
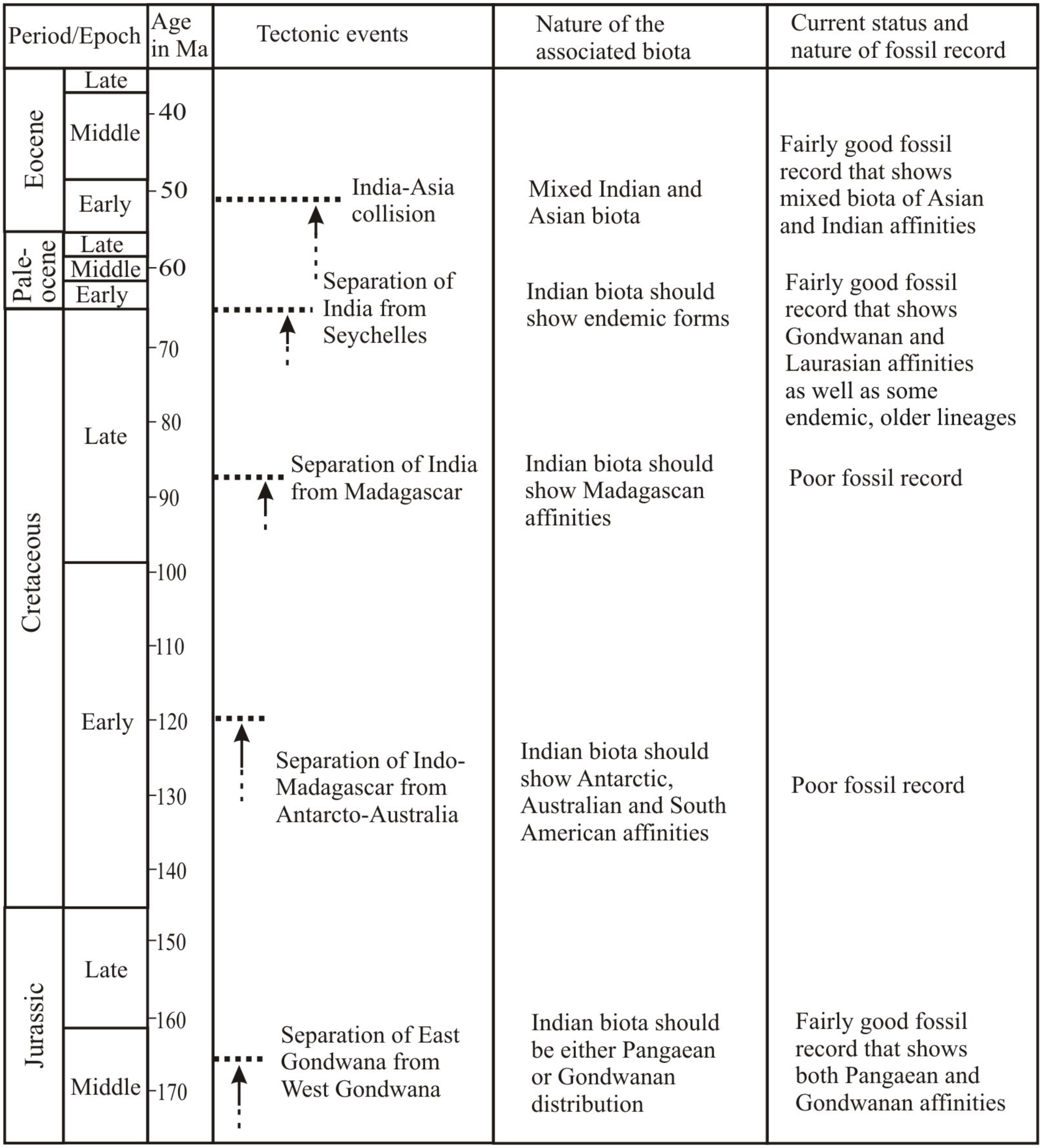


FIGURE 4. Recent paleogeographic reconstructions for the Indian plate for 120 Ma (**A** and **D**); 83.5 Ma (**B**); 80 Ma (**E**); 67.7 Ma (**C**); and 65 Ma (**F**). A-C modified after Ali and Aitchison (2008), D-F after Chatterjee et al. (2013).



Period/Epoch		Age in Ma	Tectonic events	Nature of the associated biota	Current status and nature of fossil record
Eocene	Late				
	Middle	40			
	Early	50	India-Asia collision	Mixed Indian and Asian biota	Fairly good fossil record that shows mixed biota of Asian and Indian affinities
Pale-ocene	Late				
	Middle	60			
	Early		Separation of India from Seychelles	Indian biota should show endemic forms	Fairly good fossil record that shows Gondwanan and Laurasian affinities as well as some endemic, older lineages
Cretaceous	Late	70 80 90	Separation of India from Madagascar	Indian biota should show Madagascan affinities	Poor fossil record
	Early	100 110 120 130 140	Separation of Indo-Madagascar from Antarcto-Australia	Indian biota should show Antarctic, Australian and South American affinities	Poor fossil record
Jurassic	Late	150 160			
	Middle	170	Separation of East Gondwana from West Gondwana	Indian biota should be either Pangaean or Gondwanan distribution	Fairly good fossil record that shows both Pangaean and Gondwanan affinities

FIGURE 5. Mesozoic and Cenozoic chronology, main tectonic events related to the breakup of the Indian plate from Gondwana and its collision with Asia, expected affinities of the biota, and status and affinities of the fossil record.

Osteoglossiformes, Salmoniformes, Tetraodontiformes, Siluriformes, Perciformes, Serranidae, Clupeidae, Enchodontidae, Nandidae, Labridae, Sphyrenidae, Ostracionidae, Percoidei, Pristolepidae, Clupeidae and Nandidae (e.g., Khosla and Sahni, 2003; Prasad, 2012; Khosla and Verma, 2015). This fauna was suggested to have none or little biogeographic significance. However, some taxa like *Igdabatis* (Myliobatidae) and *Rhombodus* sp. (Rhombodontidae) are of particular interest, as these forms are also described from the Maastrichtian of Niger and the Campanian to Maastrichtian of Spain, which are indicative of Late Cretaceous shallow marine connections between these landmasses.

The Maastrichtian anuran fossil record consists of Myobatrachidae, ?Leptodactylidae or Hemisotidae, Pelobatidae, Discoglossidae (Gobiatinae), Ranoidea and ?Hylidae, which were recovered from the Deccan volcanic province (Sahni et al., 1982; Prasad and Rage, 2004; Prasad, 2012). The families Myobatrachidae (*Indobatrachus*), ?Leptodactylidae, ?Hylidae and Ranoidea from India are considered Gondwanan clades, also known from South America and Africa (Duelman and Trueb, 1986; Sanchiz, 1997). Interestingly, living myobatrachids occur in Australia and Papua-New Guinea; thus, it has been proposed that myobatrachids reached India from South America via northern Antarctica (Spinar and Hodrová, 1985). The pelobatid and Gobiatinae discoglossid frogs are considered to represent the first occurrence of Laurasian faunal elements in India, as these frog groups are widely recorded from Central Asia, Europe and North America (Prasad and Rage, 1995; Khosla, 2014).

The fossil record of lizards is poorly documented from India, with a limited record from the Deccan volcanic province represented by very fragmentary material. The lizard fossils of India have been referred to the Anguidae, *Eolacertilia*, Iguanidae, Scincidae, Xenosauridae, some indeterminate lacertilians and gekkonid eggshells (Prasad and Rage, 1995; Prasad, 2012). The occurrence of the Anguidae in the Maastrichtian of India indicates the presence of a Laurasian faunal element because it has a restricted Late Cretaceous to early Tertiary distribution in Central Asia, China, Europe and North America. On the contrary, the taxonomic validity of Indian fossils identified as Eolacertilia, Iguanidae, Scincidae and Xenosauridae is considered to be doubtful (Prasad, 2012).

The Maastrichtian snakes of India are represented by ?Nigerophiidae (*Indophis sahnii* Rage and Prasad, 1992), Madtsoiidae (*Sanajeh indicus* Wilson et al., 2010 and *Madtsoia pisdurensis* Mohabey et al., 2011), Aniliidae (*Coniophis*) and Serpentes (Rage et al., 2004; Wilson et al., 2010; Prasad, 2012). This snake fauna was recovered from the Deccan volcanic province. Among these snake taxa, the ?Nigerophiidae and Madtsoiidae have great paleobiogeographic interest, as these are Gondwanan clades previously recorded in South America, Madagascar and Niger (Rage and Prasad, 1992; Wilson et al., 2010; Mohabey et al., 2011).

A fairly good fossil record of turtles is known from the continental Maastrichtian deposits of the Cauvery Basin and the Deccan volcanic province. It consists of pelomedusoid, bothremydid and podocnemidid turtles. The bothremydids include *Carteremys leithii* Carter, 1852, *Carteremys pisdurensis* Jain, 1977, *Sankuchemys sethnai* Gaffney et al., 2003, *Kurmademys kallamedensis* Gaffney et al., 2001 and *Taphrosphys* sp., while podocnemidids consist of *Shweboemys pisdurensis* Jain, 1986 (Jain, 1977, 1986; Gaffney et al., 2001, 2003; de Lapparent de Broin et al., 2009). Gaffney et al. (2009) argued that three bothremydid turtles, *Kurmademys* and *Sankuchemys* from the Maastrichtian of India, as well as *Kinkonychelys* from the Late Cretaceous of Madagascar, are nested in a single clade (Kurmademydini) and have a sister-group relationship to each other. Furthermore, the Kurmademydini are regarded as closely related to the Cerachelyini, which are recorded from the variously dated Cretaceous Santana Formation of Brazil and the Cenomanian Kem Kem deposits of Morocco (Sahni, 2010). It is well documented that Indian Maastrichtian pelomedusoids represent a Gondwanan lineage, which would have been separated from the ancestral stock at the time of the India/Africa split (de Broin, 1988).

The recorded crocodilian fauna of India includes Dyrosauridae, Crocodylia (*Crocodylus* sp.), and Notosuchia (cf. *Simosuchus*), described from the Maastrichtian deposits of the Deccan volcanic province and the Cauvery Basin (Khosla et al., 2009; Prasad, 2012; Prasad et al., 2013; Prasad et al., 2015). In addition, Prasad and de Lapparent de Broin (2002) carried out a detailed and exhaustive comparative analysis of crocodilian teeth from the Deccan volcanic province and found that the teeth are morphologically close to those of ziphodont crocodiles such as *Hamadasuchus*, from the Early Cretaceous of Africa, and *Mahajangasuchus*, from the Late Cretaceous of Madagascar. More recently, Prasad et al. (2013) stated that *Simosuchus* sp. from India represents the first occurrence of the group outside the Late Cretaceous of Madagascar. Apart from the Indian record, Wilson et al. (2001) described a baurusuchid crocodile (*Pabwehshi pakistanesis* Wilson et al., 2001), of South American affinities, from the Maastrichtian Pab Formation in Eastern Balochistan, Pakistan. Overall, the crocodile record of India strongly indicates a Gondwanan provincialism.

Dinosaurs are a significant component of the Late Cretaceous vertebrate assemblages of India. The Maastrichtian deposits of the Deccan volcanic province, Cauvery Basin and the Khasi Group have yielded bones of sauropods and theropods, as well as nests, eggs and eggshell fragments of sauropods, theropods and ornithopods (von Huene and Matley, 1933; Sahni and Khosla, 1994b; Loyal et al., 1996; Jain and Bandyopadhyay, 1997; Khosla, 2001; Vianey-Liaud et al., 2003; Wilson and Upchurch, 2003; Khosla et al., 2004; Goswami et al., 2013; Fernández and Khosla, 2015). The sauropod comprises titanosaurids such as *Jainosaurus septentrionalis* (von Huene and Matley, 1933) and *Isisaurus colberti* (Jain and Bandyopadhyay, 1997), whereas theropods include abelisaurids such as *Indosuchus raptorius* (von Huene and Matley, 1933), *I. matleyi* (von Huene and Matley, 1933), *Laevisuchus indicus* (von Huene and Matley, 1933), *Lametasaurus indicus* (Matley, 1923), *Rajasaurus narmadensis* (Wilson et al., 2003), *Rahiolisaurus gujaratensis* (Novas et al., 2010) and ?maniraptoran troodontids (von Huene and Matley, 1933; Chatterjee, 1978; Hunt et al., 1994; Chatterjee and Rudra, 1996; Jain and Bandyopadhyay, 1997; Wilson and Upchurch, 2003; Wilson et al., 2003; Novas et al., 2010; Goswami et al., 2013). The sedimentary beds associated with the Deccan volcanic province occur in central and western India; they have only yielded nests, eggs and eggshell fragments of dinosaurs; currently, these remains are placed into four oofamilies: Megaloolithidae, Fusioolithidae, Laevisoolithidae and Elongatoolithidae (Khosla and Sahni, 1995; Fernández and Khosla, 2015).

Titanosaurids are not useful from a paleobiogeographic point of view as the group had already achieved a global distribution by the Early Cretaceous (Wilson, 2005). On the other hand, the Indian abelisaurids, *Rajasaurus* and *Rahiolisaurus*, are considered to have close phylogenetic affinities with *Majungasaurus* and *Carnotaurus* from the Late Cretaceous of Madagascar and South America, respectively (Wilson et al., 2003; Novas et al., 2010). However, the presence of possible maniraptoran troodontids in the Late Cretaceous of India is anomalous, as their previous record was restricted to Europe, Asia and North America (Goswami et al., 2013). In addition, the comparison of Indian Late Cretaceous eggshell-based dinosaur taxa shows a close resemblance with oospecies known from France, Spain, Africa and Argentina (Loyal et al., 1998; Khosla and Sahni, 2003; Vianey-Liaud et al., 2003; Fernández and Khosla, 2015).

Cretaceous mammals are only known from the Maastrichtian deposits of the Deccan volcanic province and the Cauvery Basin of India. They are represented by haramiyidians, gondwanatherians, and eutherians (Prasad et al., 2010; Goswami et al., 2011; Prasad, 2012; Verma et al., 2012a). The eutherians include adapisoriculids (*Deccanolestes hislopi* Prasad and Sahni, 1988, *D. robustus* Prasad et al., 1994, *D. narmadensis* Prasad et al., 2010 and possibly *Sahnitherium rangapurensis* Rana and Wilson, 2003), ?otlestids and archaic ungulates (*Kharmerungulatum vanvaleni* Prasad et al., 2007a); they represent the only undisputed pre-Tertiary eutherian mammal record from Gondwana landmasses (Prasad and Sahni, 1988; Prasad et al., 1994, 2007a, 2010; Rana and Wilson, 2003; Khosla et al., 2004; Boyer et al., 2010; de Bast et al., 2012). The gondwanatherians are known by Sudamericidae such as *Bharattherium bonapartei* Prasad et al., 2007b (=*Dakshina jederi* Wilson et al., 2007) and a second unnamed taxon, Sudamericidae indeterminate (Krause et al., 1997; Prasad et al., 2007b, Wilson et al., 2007; Verma et al., 2012b). Haramiyidians comprise *Avashishta bacharamensis* (Anantharaman et al. 2006); it is the only known record from the Late Cretaceous of India and is regarded as a Gondwanan relict of the Laurasian haramiyidians (Anantharaman et al., 2006). Surprisingly, *Deccanolestes*, the Indian adapisoriculid, appears more close to *Afrodon*, the adapisoriculids known from the late Paleocene of Africa and Europe, while the archaic ungulate *Kharmerungulatum* is close to *Protungulatum*, an earliest definitive ungulate from the early Paleocene of North America (Prasad et al., 2007a, 2010; Goswami et al., 2011). Based on the older age and primitive morphology of the Indian eutherians such as *Deccanolestes* and *Kharmerungulatum*, it has been suggested that these eutherian mammals evolved on the drifting Indian plate, and adapisoriculids may have dispersed from India to Africa by the Cretaceous/Paleocene transition (Prasad et al., 2007a, 2010).

Sudamericid gondwanatherians are an extinct group of allotherian mammals of exclusive Gondwanan distribution. They are known from the Late Cretaceous to Eocene of South America, Late Cretaceous of Madagascar, probable Cretaceous of Tanzania (Africa) and middle Eocene of Antarctica (Verma et al., 2012a, and references cited). The broad geographic distribution of sudamericid mammals in the Maastrichtian of India, together with the inferred sister-group relationship with Madagascan forms, supports the cosmopolitan distribution of the group and further suggests some Late Cretaceous connections among the Gondwana landmasses. On the other hand, haramiyidians are considered as a Laurasian group as their oldest reports were known from the Late Triassic to Middle Jurassic of Europe and North America. However, these are also documented from the Late Jurassic of Tanzania and the Early Cretaceous of Morocco in Africa (Anantharaman et al., 2006). The Indian haramiyid, *Avashishta bacharamensis*, is morphologically close to *Allostaffia aenigmatica* Heinrich, 1999, a Late Jurassic haramiyid from Tanzania.

Maastrichtian Non-Vertebrate Record

It is worth mentioning that the Maastrichtian sediments of the Deccan volcanic province have yielded some significant non-vertebrate remains that can be used to understand the biogeographic position of the Indian plate during the Late Cretaceous. These fossil finds include one of oldest global records of freshwater diatoms, members of the families/tribes Poaceae (grasses), Oryzeae (rice) and Vitaceae (grapes), and highly endemic ostracod assemblages (Ambwani et al., 2003; Sharma and Khosla, 2009; Whatley, 2012; Manchester et al., 2013; Khosla, 2015; Khosla et al., 2015). These biotic elements were suggested to have probably originated and diversified in the northward drifting Indian plate by the end of the Cretaceous (Khosla, 2014; Khosla and Verma, 2015).

CONFRONTING THE DATA: PALEONTOLOGICAL VS. GEOPHYSICAL

During the Cretaceous, the configuration of India was dynamic as it detached from East Gondwanan landmasses, and the detached Indian plate drifted northward from Antarctica and Australia towards the Equator across the Tethys Sea, until its final collision with Asia (Chatterjee et al., 2013). This rift and drift is thought to have led to the opening of the Indian Ocean, the closing of the Tethys Sea and the development of a highly endemic biota on the Indian plate (Whatley, 2012). The last three decades have witnessed the extensive and focused work on expanding the record of fossil vertebrates from the Upper Cretaceous deposits of India (e.g., Khosla and Verma, 2015). As currently understood, the Late Cretaceous, particularly Maastrichtian, vertebrate fossil record of India seems to have belonged to three distinct faunal domains, namely Gondwanan, Laurasian and an endemic or older one. In marked contrast, geophysical studies have also made tremendous strides in the last three decades in order to better document the history of Gondwana fragmentation and geodynamics of the Indian plate (e.g., Smith et al., 1981, 1994; Hay et al., 1999; Ali and Aitchison, 2008). As a result, various inferences have been drawn based on these studies, and many hypotheses have been proposed to explain the presence or absence of physical connections related to the northward drifting Indian plate with adjacent landmasses.

During the Berriasian to early Albian interval, the India and Madagascar block fragmented from Australia and Antarctica and started their northward displacement. The western, southern and eastern margins of the Indo-Madagascar block were occupied by seas. The fossil record of this interval, mostly consisting of a few fishes and shallow marine reptiles known from the coastal regions of Andhra Pradesh and Gujarat, not only supports the geophysical interpretation, but also indicates the existence of marine transgressions concomitant with rising sea level. Some of the marine fish faunas seem to be close to those known from the Berriasian to Cenomanian deposits of Morocco (Baksi, 1973).

Recently, a reasonably good amount of vertebrate fossil data has emerged from the Cauvery and Narmada basins (Verma, 2015). Nevertheless, the record is mostly marine in nature and includes several new taxa of fish, coming from the Cenomanian-Turonian deposits of the basins and corresponds approximately to the time when India was separated from its sister island-continent Madagascar. Many shark taxa such as *Squalicorax*, *Dwardius*, *Cretalamna*, *Eostriatolamia*, *Cretodus* and *Ptychodus* have also been recorded from coeval deposits of Australia and Africa (Cappetta, 2012). Some of these taxa are also known from the latest Cretaceous (Maastrichtian) deposits of Madagascar and Antarctica (Cappetta, 2012). Interestingly, a majority of shark taxa of the Cauvery Basin have been previously recorded from high palaeolatitudes at sites belonging to both hemispheres, thus suggesting an antitropical distribution, with cooler water preferences of these taxa, and also placing India in a high palaeolatitude position in the Southern Hemisphere during the Cenomanian-Turonian (Underwood et al., 2011; Verma et al., 2012b). The presence of these taxa in southeastern (Cauvery Basin) and western (Narmada Basin) India, indicate major sea level fluctuations and epicontinental seaways; these transgressive episodes during the Cenomanian-Turonian in India may have dispersed these taxa into the continental interior lowland regions (Verma, 2015). In addition to vertebrates, the occurrences of the ammonite *Placenticeras* (Placenticeratidae) from the Cenomanian-Turonian deposits of the Bagh Formation (Narmada Basin), Madhya Pradesh, Central India shows significant resemblance with those known from the coeval deposits of northernmost Madagascar and southernmost Africa. This indicates that the Indo-Madagascar block remained physically united till this time and connected with Africa by shallow seas (Bardhan et al., 2002).

Geophysical data suggest that the northward drifting of the Indian plate led to its physical isolation after its separation from Madagascar during the Turonian, thus suggesting that its on board biota from the Turonian to the Maastrichtian (ca. 90 to 66 Ma) must have been highly endemic to the Indian subcontinent by those times. However, fossil data from this interval, mostly known for the Maastrichtian, show mixed elements of Gondwanan and Laurasian affinities, as well as some of older, highly endemic forms. In order to account for such discrepancies, both southern and northern dispersal models have been advanced for the drifting Indian plate (Sahni, 1984; Krause et al., 1997; Hay et al., 1999; Chatterjee and Scotese, 1999, 2010; Prasad and Sahni, 1999, 2009; Case, 2002; Rage, 2003; Ali and Aitchison, 2008; Prasad et al., 2010; Chatterjee et al., 2013).

The peculiar vertebrate faunas described for the Maastrichtian of India include forms such as myliobatid fish; myobatrachid, leptodactylid, hylid and ranoid frogs; nigerophiid and madtsoiid snakes; bothremydid turtles; notosuchian and baurusuchid crocodiles; sudamericid mammals and abelisaurid dinosaurs. These were interpreted as Gondwanan faunas, which were specifically shared with Madagascar, South America, and Africa (e.g., Khosla and Verma, 2015). Among these vertebrates, the bothremydid turtles like *Kurmademys* and *Sankuchemys* from Madagascar and India, respectively, have a sister-group relationship (Gaffney et al., 2009), whereas the gondwanatherian mammals such as *Lavanify* and *Bharattherium* from the Late Cretaceous of Madagascar and India also form a sister-group (Krause et al., 1997). The discovery of *Simosuchus*-like notosuchian crocodiles from India is the first report of the group outside the Late Cretaceous of Madagascar (Prasad et al., 2013). Numerous dispersal scenarios have been proposed to explain the presence of these faunal elements in India during the late Cretaceous (Maastrichtian). They include sub-aerial connections between Indo-Madagascar and South America via Antarctica through the Kerguelen Plateau (physical connection with India) and Gunnerus Ridge (physical connection with Madagascar), up to 80 Ma (Krause et al., 1997; Hay et al., 1999; Case, 2002). It has also been suggested that a land connection between India and Africa was established through Greater Somalia, from the Late Cretaceous to the Eocene (Chatterjee and Scotese, 1999). Also, sub-aerial connections between South America and India through Antarctica, via the Ninetyeast Ridge-Kerguelen Plateau in the Late Cretaceous (Chatterjee and Scotese, 2010), have been suggested. Additional dispersal routes between India and Africa have been suggested, via the Oman-Kohistan-Dras Island Arc at the Cretaceous/Paleocene transition (Chatterjee et al., 2013). Indo-Madagascar and African dispersal corridors may have existed by 88 Ma, consisting of modern day submerged aseismic tectonic elements comprising the Mascarene Plateau and the Chagos-Laccadive Ridge (Sahni, 1984). Other proposed links include a land connection between India and Africa through Madagascar comprising a central corridor by 65 Ma (Briggs, 2003), a terrestrial link between India and Madagascar via the Seychelles Plateau at the close of the Late Cretaceous ca. 66 Ma (Averianov et al., 2003; Rage, 2003), as well as a discontinuous land connection between India and Africa via the Seychelles block-Amirante Ridge-Providence bank-northern tip of Madagascar and east coast of Madagascar that existed in the Late Cretaceous, ca. 83.5 Ma (Ali and Aitchison, 2008).

Several authors have suggested a southern dispersal model, in which South America and Indo-Madagascar were indirectly connected via Antarctica through the Kerguelen Plateau until 80 Ma; this inference was mainly drawn from the Cretaceous paleogeographic reconstruction proposed by Hay et al. (1999) to explain the presence of Late Cretaceous Gondwanan faunal elements in South America, Madagascar and India (e.g., Krause et al., 1997; Prasad and Sahni, 2009). More recently, based on geological and geophysical data, it has been proposed that during the Late Cretaceous, large portions of the Kerguelen Plateau were submerged, while only a few sections were sub-aerially exposed; its margins would have been separated by an extensive, more than 300 km long stretch of deep-sea waters and, hence, it could not have served as a physical connection for faunal interchanges (Ali and Aitchison, 2008, 2009). A similar explanation has also been advanced for the Gunnerus Ridge land connection (Ali and Krause, 2011). Furthermore, on the basis of phylogenetic studies, Ali and Krause (2011) demonstrated that the presence of medium- to large-sized land vertebrates such as abelisaurid theropod and titanosaurian sauropod dinosaurs, as well as notosuchian crocodiles in India and Madagascar, indicate that these vertebrates had long ghost lineages, which would have been present in the Early Cretaceous in Gondwana. Therefore, their ancestors reached Indo-Madagascar prior to its physical separation from the rest of the Gondwana landmasses. In other words, this is a lateral variant of the "pan-Gondwana" model of Sereno et al. (2004). Nevertheless, these authors offer no view to explain the presence of small mammals like sudamericid gondwanatherians in Indo-Madagascar only.

Abelisaurid dinosaurs are largely regarded as endemic to Gondwana, and considered to have a significant role for understanding the Cretaceous biogeography of Gondwana (Sampson et al., 1998; Sereno et al., 2004). To account for the absence or presence of abelisaurids in the Cretaceous of Africa, two alternative models have been proposed, namely "Africa-first" and "pan-Gondwana" (e.g., Sereno et al., 2004). The "Africa-first" model holds that the absence of abelisaurids in Africa and their presence in South America, India and Madagascar indicates that the group appeared sometime in the Early Cretaceous in Gondwana after the physical isolation of Africa (Sampson et al., 1998). In contrast, the later discovery of abelisaurids in the Aptian-Albian and Cenomanian of Africa by Sereno et al. (2004) led these authors to conclude a pan-Gondwanan distribution for the group. The "pan-Gondwana" model favors a pre-Late Cretaceous origin of abelisaurid dinosaurs in Gondwana and suggests that three narrow and intermittent passages existed between major Gondwana landmasses: (1) the Walvis Ridge and Rio Grande Rise between South America and Africa; (2) the Palmer Land Block and South Georgia island terrane between South America and Antarctica; and (3) the Kerguelan Plateau and Gunnerus Ridge between Antarctica and Indo-Madagascar during the Late Cretaceous, ca. 97 Ma (Sereno et al., 2004; Sereno and Brusatte, 2008). The main difference in these two models is the timing of the South America and Africa split, which was nicely dealt with by Krause et al. (2006). Relevant to these models in the Indian context is that abelisaurids had a Gondwanan distribution and that the group reached a united Indo-Madagascar block from South America via Antarctica and the Kerguelan Plateau and Gunnerus Ridge before ca. 97 Ma. This is consistent with the latest paleogeographic reconstructions proposed by Ali and Aitchison (2008, 2009) and Ali and Krause (2011).

Sahni (1984) proposed a dispersal corridor between Indo-Madagascar and Africa by 88 Ma, which has now been clearly refuted (Prasad and Sahni, 2009). Such a corridor was based on tectonic elements such as the Mascarene Plateau and the Chagos-Laccadive Ridge. However, Subrahmanya (1998) argued that these features were formed in the Indian Ocean during the Paleocene, ca. 62 Ma, and hence were not available to connect India and Madagascar to Africa in the Late Cretaceous. A more recent proposal by Ali and Aitchison (2008) suggesting a Maastrichtian discontinuous land connection between India and Madagascar via the Seychelles block-Amirante Ridge-Providence bank seems less appealing. The most common shared Maastrichtian vertebrates of India and Madagascar are abelisaurid dinosaurs, bothremydid turtles, madtsoiid snakes, notosuchian crocodiles and sudamericid mammals. Notosuchian crocodiles and sudamericid mammals were non-meat-eating animals (Koenigswald et al., 1999; Buckley et al., 2000) and, thus, they would have not been able to traverse large marine barriers. It could be possible that small-sized sudamericid mammals might have rafted from Madagascar to India, however, the record of paleo-oceanic currents is not available from this part of the Indian Ocean. Abelisaurid dinosaurs were large land animals and must have not been capable of crossing extensive marine conditions. On the other hand, the occurrences of freshwater bothremydid turtles and madtsoiid snakes are of vertebrates intolerant of deep sea conditions. According to the Ali and Aitchison (2008) model, the dispersal of vertebrates from Madagascar to India involves the crossing of extensive shallow to deep marine waters over a stretch about 800-900 km long. However, during the late Cretaceous, the sea level was high, the actual sub-aerial exposures of the Seychelles block, Amirante Ridge and Providence bank are not fully documented and vertebrates involved in dispersal were nonmarine, thus the proposal appears less likely to explain Maastrichtian faunal similarities between India and Madagascar.

To explain the presence of faunas with Laurasian affinities like pelobatid and discoglossid frogs, anguimorph lizards and some other microfossils consisting of charophytes and palynomorphs in the Maastrichtian of India, an early India/Asia collision, sub-aerial connection between India and Asia and sweepstakes dispersal models have been proposed (Jaeger et al., 1989; Bhatia et al., 1996; Prasad and Sahni, 1999; Khosla, 2014). The early India/Asia collision model of Jaeger et al. (1989) proposed that the collision between India and Asia occurred by the Cretaceous-Paleocene boundary, thus facilitating biotic exchanges between these two landmasses. However, current geophysical data do not favor an end-Cretaceous age for India/Asia collision; instead, it suggests a much younger collision age and hence the early India/Asia dispersal is no longer considered as a valid model for faunal migrations (e.g., Ali and Aitchison, 2008; Khosla and Verma, 2015). Subsequently, Bhatia et al. (1996) argued that the faunal exchange from Asia to India would have been taken place by way of "landspans" (features of rifting continents, like island arcs) and other crustal blocks, such as the Kohistan-Dras Island arc systems and the Iran-Afghanistan blocks. Alternatively, Prasad and Sahni (1999) noted that faunal elements involved in the exchange were small-sized. These authors modified the dispersal model proposed by Bhatia et al. (1996) and suggested that the faunal exchange probably occurred through filter corridors/sweepstakes from Asia to India across the Tethyan Sea. It is worth mentioning that the bulk of geophysical data suggests that during the Late Cretaceous (Maastrichtian), the marine gap between northern India and Asia was too wide and would have been impossible for land animals to cross. In addition, some workers also opposed the northern connections of India with Asia based on the fact that the fossil record of Laurasian faunal elements is poor, represented only by fragmentary material and hence their biogeographic implications are uncertain (e.g., Thewissen and McKenna, 1992; McKenna, 1995). Considering that the known fossil record is valid, the model proposed by Prasad and Sahni (1999) could be one of the most suitable explanations for the presence of Lauasian faunal elements in India. More recently, Ali and Aitchison (2008) postulated that the intra-Tethyan island arc would have fueled sweepstake dispersals by providing "landspans." However, these authors find the Late Cretaceous prevailing atmospheric winds as well as oceanic surface currents unfavorable for a sweepstake dispersal model.

Paleontological data, including the oldest global records of adapisoriculid (*Deccanolestes*) and archaic ungulate (*Kharmerungulatum*) mammals, freshwater diatoms, Poaceae grasses, Oryzeae (rice), Vitaceae (grapes), as well as highly endemic ostracod assemblages from the Maastrichtian of India provide evidence compatible with the geophysical data. These taxa are restricted to India, and could be interpreted as part of a biota endemic to or oldest in India. It is possible that these lineages evolved in the long northward drifting of the Indian plate during the Late Cretaceous, in isolation, after its separation from Madagascar (e.g., Khosla and Verma, 2015). Interestingly, the discovery of taxa such as myliobatid (*Igdabatis*) and rhombodontid (*Rhombodus*) fishes, troodontid dinosaurs and adapisoriculid (*Deccanolestes*), haramiyid (*Avashishta*) and sudamericid mammals, related to Africa and/or Europe/Laurasia from the Maastrichtian of India, suggest faunal exchanges between these landmasses (e.g., Prasad and Sahni, 2009; Goswami et al., 2011, 2013). Briggs (1989, 2003) proposed that after separating from Madagascar, the Indian plate came close to northeast Africa, and biotic links may have developed between them through the Somali Peninsula during the Late Cretaceous. Chatterjee and Scotese (1999) also maintained that the faunal exchanges would have been occurred between India and Africa through Greater Somalia in the Maastrichtian. More recently, Chatterjee and Scotese (2010) and Chatterjee et al. (2013) rejected the "Greater Somalia" model, and instead introduced a new one for the Maastrichtian India-Africa connection; this time, by means of suggested "landspans" such as the Oman-Kohistan-Dras Island Arc between these landmasses. Assuming this model is correct, it favors bidirectional faunal dispersals based on the following facts. First, the report of the oldest adapisoriculid mammals from the India and their close phylogentic affinities with those known from the late Paleocene of Africa and Europe, indicating possible dispersal from India to Africa (Prasad et al., 2010; Goswami et al., 2011). Second, the presence of myliobatid (*Igdabatis*) and rhombodontid (*Rhombodus*) fishes and troodontid dinosaurs in the Maastrichtian of India having close resemblance with the same forms known from stratigraphically older horizons in Africa and Europe/Laurasia, which are possible indicators of Africa to India dispersal events. Two observations should be made regarding this model:

1. The timing of the Kohistan-Dras Island Arc collision with Asia and India. Some authors proposed that the Kohistan-Dras Island Arc first collided with India ca. 95-65 Ma (e.g., Chatterjee et al., 2013). Alternatively, other authors suggest that the Kohistan-Dras Island Arc first collided with Asia by 102-75 Ma (e.g., Rehman et al., 2011). Although the collision timing of the Kohistan-Dras Island Arc with India/Asia is still a matter of debate, if the later dates are correct then this model does not work.

2. The nature of paleo-oceanic currents of this part of the Indian Ocean. Based on paleogeographic reconstructions and paleo-oceanographic modeling, Ali and Huber (2010) found that surface currents were favorable for biotic dispersal from Africa towards Madagascar during the Paleogene. Indeed, Late Cretaceous paleo-oceanographic data of this part of the Indian Ocean are not available; if the paleo-oceanographic currents had a similar pattern during the Late Cretaceous, then it would be difficult to admit a dispersal event from India to Africa.

Molecular studies have made numerous attempts to explore the possible role of the northward drifting Indian plate as a "Noah's Ark" (Fig. 4). Based on molecular analysis, it has been proposed that acrodont lizards, ratite birds, ichthyophiid caecilians, passerine birds, Asian arowana, cichlid and aplocheiloid fishes, Crypteroniaceae and Melastomataceae plants, had an ancient Gondwana origin and arrived in Asia on the rafting Indian plate at the time when the latter docked with Asia (e.g., Sparks, 2004). In addition, a few molecular studies also suggest that three clades of ranoid frogs, the Rhacophorinae, Raninae and Discoglossidae, originated on the drifting Indian plate and later dispersed to Asia (i.e., out-of-India dispersal) upon the India/Asia collision (Bossuyt and Milinkovich, 2001). Fossil evidence in favor of out-of-India dispersal is poor for the Late Cretaceous of India. Currently, there are two reports comprising fossils of an ilium referable to a ranoid frog and a crepe myrtle of the plant family Lythraceae from the Maastrichtian sediments of the Deccan volcanic province, favoring an out-of-India dispersal (Prasad and Rage, 2004; Liu et al., 2007). It is important to note that the northward drifting Indian plate also served as a "Beached Viking Funeral Ship." The presence of extinct Gondwana faunal elements such as kurmademydini turtles, abelisaurid dinosaurs, and gondwanatherian mammals on the drifting Indian plate and their absence in Asia strongly suggest that these groups became extinct before the Indian plate docked with Asia.

CAVEATS AND PROSPECTS

The first Indian Late Cretaceous vertebrate remains were discovered in the early 1930s, long before the advent of plate tectonics and geophysical models (von Huene and Matley, 1933). However, there is an abundant bibliography about the Late Cretaceous vertebrate faunas of India shared by Madagascar, South America, Africa, Europe and Asia, as well as on its endemic lineages (e.g., Khosla and Verma, 2015). It is interesting to note that the peculiar composition of these faunas attests to the complexity of its biogeographic history. In the last three decades, several authors applied both geophysical and paleontological data along with plate tectonic models to understand the rift and drift of the Indian plate from Gondwana up to its collision with Asia and associated biogeographic patterns. Prior to 2008, paleontologists turned mostly to dispersalist models, which were more or less consistent with the paleogeographic reconstruction proposed by Hay et al. (1999), in order to explain the presence of Late Cretaceous faunas having South American affinities in the Indo-Madagascar region. This model was widely accepted for more than a decade.

Recently, according to new paleogeographic reconstructions of the Indian plate, Ali and Aitchison (2008) maintained that after isolating from Australia and Antarctica, the Indo-Madagascar block lost its physical contact from the rest of Gondwana landmasses. As a result, a "pan-Gondwana" distribution model was advanced in order to explain the Late Cretaceous faunal uniqueness of South America, Africa and Indo-Madagascar. This model appears to be also consistent with the paleogeographic reconstructions of Scotese (2001) and Smith et al. (1994). Assuming that the during the Late Cretaceous, most portions of the Kerguelen Plateau were below sea level, as argued by Ali and Aitchison (2008), the existence of a sub-aerial connection between South America and India through Antarctica via Ninetyeast Ridge-Kerguelen Plateau seems less likely in the Late Cretaceous (Chatterjee and Scotese, 2010). The proposal of a Seychelles block, Amirante Ridge and Providence Bank intermittent connection between India and Madagascar also appears less likely, if the dispersal capabilities, habitat, and sea level change are taken into consideration. The absence of troodontid dinosaurs and adapisoriculid and archaic ungulate mammals in the Maastrichtian of Madagascar favors a "pan-Indo-Madagascar" distribution for the faunas shared by India and Madagascar or are indicative of the existence of an unrecognized dispersal corridor between them, as suggested by Mohabey et al. (2011).

The Maastrichtian vertebrate fossil record also suggests that an influx of faunas from India to Africa or vice versa during the latest Cretaceous is likely because the fossil record of this interval shows taxa in common with some African and European/Laurasian associations (Prasad et al.. 2010; Goswami et al., 2011, 2013; Khosla, 2014). The faunal dispersal through the Oman-Kohistan-Dras Island Arc between India and Africa is a highly attractive model. However, the timing of the initial collision of this Island Arc with Asia and India is still a matter of debate. The latest Cretaceous faunal exchanges between Asia and India by the means of filter corridors/ sweepstakes through some intervening landspans such as an intra-Tethyan island arc are consistent with recent paleogeographic reconstructions (Ali and Aitchison, 2008). However, the fragmentary nature of the fossil record doesn't allow a conclusive analysis. The Maastrichtian fossil record of oldest or endemic biotic elements like adapisoriculid and archaic ungulate mammals, diatoms, grasses, rice, grapes and ostracods, further suggest that the northward drifting of the Indian plate served as a plausible "Noah's Ark," and that these elements could have been a product of its isolation. Furthermore, the occurrences of Gondwana biota on the Indian plate and their absence in Asia indicate that the Indian plate also acted as a "Beached Viking Funeral Ship" during its northward journey. The presence of ranoid frogs and crepe myrtle plants in the Maastrichtian of India likewise suggest that the Indian plate also transported Gondwanan biota into Asia upon its docking –the "Docked Noah's Ark" model. It is worth mentioning that the above-mentioned biogeographic models such as "Noah's Arks," "Docked Noah's Ark" and "Beached Viking Funeral Ship" are compatible with the geophysical data currently known for the Indian plate.

The precise timing of separation of the Indian plate from the rest of the Gondwana landmasses, its dispersal and collision with Asia along with the actual shape and size of the drifting Indian plate prior to collision, are geophysically less understood (e.g., Powell et al., 1988; Ali and Aitchison, 2005; Jokat, 2010). In addition to this, the biogeographic role of seamounts and volcanic arcs (landspans) has not been fully explored for the Indian plate in geophysical and tectonic terms (Hay et al., 1999; Ali and Aitchison, 2005; Chatterjee et al., 2013).

The Cretaceous paleontological record of terrestrial vertebrates of India is fairly documented for the Maastrichtian epoch; however, this Maastrichtian record alone fails to explain the whole Cretaceous biogeographic history of the Indian plate. The pre-Maastrichtian record is extremely poor and represented only by a few marine vertebrates. This marine fossil record is definitely not enough data for a detailed understanding of the biogeographic history of the Indian plate. The main reasons behind our (currently) restricted fossil record are: (1) Cretaceous deposits have been poorly sampled by paleontologists, as there are less numbers of Indian paleontologists working on these groups and time interval, and (2) the yield of fossils from Cretaceous deposits is poor due to some preservation bias.

Geophysical data and paleogeographic reconstructions of the Gondwana fragmentation in general, and of the Indian plate in particular, are continuously evolving. As a result, older dispersal models and paleogeographic reconstructions have periodically been replaced by newer ones. In the light of the above-mentioned observations, we hope that new paleontological data from the Cretaceous deposits of India, as well as new geophysical information on the rifting and drifting of India from Gondwana and its collision with Asia, will be generated at a finer resolution in the near future; this will help to better document and analyze the biogeographic history of the Indian plate.

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