The Indian plate has a long history of rifting, drifting and collision. It travelled for about 9000 km from its position within Gondwana to reach its present position within Asia. During its northward journey, the Indian landmass remained physically isolated for about 35 Ma from all other landmasses after its final break-up from Madagascar. A critical examination of the vertebrate fossil record of the Indian plate for the period of early and late drift phases offers very limited information for the early drift phase, but reveals a complex biogeographic history for the late drift phase. The fauna of late drift phase is represented by taxa of both Gondwanan and Laurasian affinities and some endemic forms that originated in the Indian subcontinent and later dispersed out of it. The close relationship between different Late Cretaceous vertebrate clades of the Indian subcontinent and Madagascar is explained through dispersal over a terrestrial route consisting Seychelles, Amirante Ridge, Providence Bank, and some microcontinental fragments. On the other hand, the presence of Laurasian taxa in the Late Cretaceous of the India is accounted by the island arcs and oceanic islands that existed to the north of Greater India in the Late Cretaceous. In other words, the Indian plate served as a ‘stepping stone’ between Madagascar and Laurasia.

Introduction

The modern day fauna of the Indian subcontinent is a mixture of ancestral Gondwanan clades, Laurasian immigrants, and endemic radiations resulting from its past journey from a southern high latitude position to its present position north of the equator. But how, when and what fauna migrated into or out of the Indian plate is not exactly known and hence it remains an active field of research. According to the palaeogeographic reconstructions, the supercontinent Pangea remained intact until the Late Jurassic, whereafter it started to break apart into the northern landmass of Laurasia and the southern landmass of Gondwana. This separation was slow, such that only a narrow seaway opened up between Laurasia and Gondwana. Towards the end of the Jurassic (~167 Ma) fragmentation of Gondwana into East and West Gondwana occurred (Lawver et al., 1991). East Gondwana comprised landmasses such as India, Madagascar, Antarctica, and Australia whereas West Gondwana consisted of Africa and South America (Lawver et al., 1991). Later in the Early Cretaceous (~130 Ma), the Indo-Madagascar-Seychelles block was separated from the Antarctica-Australia block. This was followed by split between India-the Seychelles from Madagascar in the Late Cretaceous (~90 Ma) (Storey et al., 1995), whereafter India drifted in isolation for about next 35 Ma at a rapid rate of about 15-20 cm/year. During this rapid drift phase, the Indian landmass passed over the Réunion hotspot in the latest Cretaceous-earliest Palaeocene as manifested by the Deccan volcanic eruptions of western and central India which led to the separation of the Seychelles from India by the Early Palaeocene (~64 Ma). Finally, the Indian plate collided with Asia between 55 and 50 Ma (Chatterjee et al., 2013, 2017 and references therein). In slight variation to this sequence of tectonic events, Chatterjee et al. (2013, 2017) opined that after breaking from Madagascar, the Indian subcontinent established links with Africa, Arabia and Europe by way of Oman-Kohistan-Ladakh Arcs at about 80 Ma, i.e., before the Deccan volcanic eruption and remained in isolation between 67 to 55 Ma (Fig. 1).

The Indian landmass, thus located in the Southern Hemisphere contiguous to South America, Africa, Madagascar, Australia, and Antarctica at the beginning of break-up of Pangaea, made the longest journey of all the continents after its separation from Gondwana to reach Asia covering almost 9000 km in about 160 million years (Chatterjee et al., 2013). During this arduous voyage, the changing position of the Indian plate aided by eustatic sea level and climate changes and volcanic activity influenced the origin, evolution, radiation, and extinction of its life forms. What happens when a landmass travels such a long distance and remains physically isolated for a major part of its journey? Did endemic fauna and flora evolve on the Indian plate during its isolation phase as was the case with Australia, Madagascar or South America? Were there any faunal exchanges between India and other landmasses during its physical
The vertebrate fauna of the syn-drift phase of India and biogeographic affinities

Early drift phase

The drift phase of the Indian plate is marked by its break-up from Gondwanan continents followed by Rajmahal volcanism in eastern India, a long interval of geographic isolation, and the eruption of Deccan Traps. During the early drift phase, as the Indian plate moved over the Kerguelen hot plume, the Indo-Madagascar block got separated from Australia-Antarctica block at about 120-130 Ma concomitant with Rajmahal volcanic eruption. This led to the development of a large sedimentary basin along its eastern coast (Vevers et al., 1991), represented today by the Cauvery Basin located in the southern Indian state of Tamil Nadu. The Cauvery Basin, due to several transgressive-regressive events, hosts marine, coastal, and fluvo-deltaic sediments of Early Cretaceous–Miocene age (Sundaram et al., 2001). Covering an area of about 25,000 km\(^2\), the Cretaceous sedimentary succession of the Cauvery basin is divisible into three groups, Uttatur, Trichinopoly and Ariyalur in this order of ascendance (Sundaram et al., 2001). The sequence is best exposed in the Ariyalur sub-basin. Though vertebrate fossils have been first reported from here in the 19th century (Egerton, 1845; Blanford, 1862; Lydekker 1879), only recently a better picture of vertebrate diversity has emerged with new discoveries from the shallow marine Karai Formation (Underwood et al., 2011; Verma et al., 2012) and the continental Kallamedu Formation (Gaffney et al., 2001; Prasad et al., 2013; Goswami et al., 2013; Halliday et al., 2016).

The vertebrate fauna of the Cauvery basin largely comes either from the early drift phase Lower Albian to Middle Turonian Karai Formation of the Uttatur Group (Blanford, 1862; Stoliczka, 1873; Lydekker, 1879; Gowda, 1967; Paul, 1973; Ayyasami and Das, 1990; Underwood et al., 2011; Verma et al., 2012), or from the late drift phase Upper Cretaceous (Maastrichtian) Kallamedu Formation of the Ariyalur Group (Lydekker, 1879; Yadagiri and Ayyasami, 1989; Gaffney et al., 2001; Prasad et al., 2013; Goswami et al., 2012, 2013; Halliday et al., 2016). In recent years, attempts have been made to ascertain the biotic affinities of the vertebrate taxa recovered from this basin (Underwood et al., 2011; Verma et al., 2012; Prasad et al., 2013; Goswami et al., 2013; Verma, 2015; Halliday et al., 2016, 2017).

The Karai Formation (Fig. 2) yielded a reasonably diverse pelagic or benthopelagic chondrichthyan fauna comprising Protosqualus sp., Gladioserratus magnus, ?Notidanodon sp., Cretalamna appendiculata, Dwardius sudindicus, ?Eostriatolamia sp., Squalicornes aff. baharijensis, Cretodus longiplicatus (Underwood et al., 2011), and Ptychodus decurrens (Verma et al., 2012). Among these, Protosqualus sp., Gladioserratus magnus, ?Notidanodon sp., Dwardius sudindicus are known from high latitude, cold water environments of northern Europe and Australia, whereas, Cretalamna appendiculata is a cosmopolitan species, and Cretodus longiplicatus was reported from both equatorial and mid-southern latitudes. The fossil reports by Egerton (1845), Stoliczka (1873), Gowda (1967) and Paul (1973) need to be re-examined before commenting on their intercontinental affinities. As per our current understanding, the chondrichthyan fauna of the Karai Formation consists largely of high latitude cool water forms restricted to northern Europe, North America and Australia with an antitropical distribution (Underwood et al.,

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Figure 1. Depicts the northward journey of India following the separation of India from Madagascar in the Late Cretaceous (modified after Powell, 1979).
This is consistent with the high latitude position of India during this time.

Although a fossil egg of a supposed chelonian was reported from the Uttatur Group, its taxonomic affinities are yet to be ascertained (Sahni, 1957). An inner mold of an indeterminate carapace and plastron of a bothremydid turtle was reported from the Karai Formation from a site near Kunnam village (Fig. 2B) (Muzzy, 1956 in Ayyasami and Das, 1990), but whereabouts of these specimens is unknown. Ichthyosaur vertebrae of the Karai Formation assigned to *Ichthyosaurus indicus* (Lydekker, 1888) and teeth referred to *Platypterygius indicus* (Underwood et al., 2011) have recently been placed in Ichthyosauria indet and Platypterygiinae indet., respectively (Prasad et al., 2017a). An isolated vertebra collected from the Odiyam Member of the Karai Formation was assigned to *Platypterygius* sp. indet. by Ayyasami et al. (2016). Platypterygiinae had a cosmopolitan distribution, with known occurrences from North America and Europe.
(England, France, Russia, and Germany) in Laurasia and Argentina, Australia and Colombia in Gondwana.

The three other sedimentary units of the early drift phase are the Lower Cretaceous Gangapur Formation of Pranhita-Godavari valley, the Lower Cretaceous Raghavapuram Mudstone of the southeast coast of India and the Lower Cretaceous Rajmahal intertrappean beds. The Kerguelen plume eruption at ~118 Ma was responsible for the formation of Rajmahal Traps of eastern India and break-up of the Indian landmass from Antarctica - Australia (Kent et al., 2002). The sedimentary layers (intertrappean) intercalated with the Rajmahal Traps (Fig. 2A) and deposited during the dormant stages of volcanism have yielded a prolific *Ptilophyllum* flora and only a single clupeiform fish *Jhingrania roonwali* (Mishra and Saxena, 1964). From the Gangapur Formation, only few actinopterygian fish teeth (*Gyrolepis* and *Caturus*-like teeth) are known (Prasad et al., 2004), whereas from the marine Raghavapuram Mudstone (Fig.3), impressions of fish scales, spines and fragmentary skeletons of Clupeiformes have been reported (Baksi, 1972). These finds, however, do not offer much on the palaeobiogeographic relationships of the Indian subcontinent during its early drift phase.

**Late drift phase**

During the late drift phase, dismemberment of Madagascar from the Indo-Seychelles block took place around ~88-90 Ma as a consequence of Marion hot plume activity. Subsequent to this, the Indian plate passed over the Réunion hotspot resulting in the eruption of Deccan Traps at the Cretaceous/Palaeogene boundary (66 Ma) and separation of the Indian landmass from the Seychelles. The fossil record of this phase comes mainly from the Bagh Group of Narmada valley, the Upper Cretaceous Lameta Formation and the intertrappean sedimentary beds of the Deccan Volcanic Province (DVP), and the Upper Cretaceous Anaipadi, Pallakkuruchchi and Kallamedu formations of the Cauvery Basin.

**Narmada Valley**

The Bagh Group of the lower Narmada valley in central India represents a sequence formed due to a marine incursion from the western margin of India in the Late Cretaceous. The Bagh Group is divided into the Nimar Sandstone, the Nodular Limestone and the Coralline or Bryozoan Limestone in this order of superposition (Jaitly and Ajane, 2013). The sequence begins with the freshwater lower part of the Nimar Sandstone which changes to marine in the upper part yielding oyster shells and shark teeth. The overlying Nodular Limestone and the Coralline Limestone are purely marine in nature and the entire sequence ranges from Cenomanian to Coniacian in age (Jaitly and Ajane, 2013). Although some shark taxa were documented from the Nimar Sandstone by Verma (1965) and Das Sarma and Sinha (1966), morphological details were not given and the illustrations were very poor. Khosla et al. (2003) documented fragmentary limb bones of a sauropod dinosaur from the red clays of the basal part of the Nimar Sandstone. Morphological features indicate close affinities to *Saltasaurus*, a titanosaur from the Late Cretaceous of Argentina.

![Figure 3. Shows the distribution of Deccan Traps in peninsular India and various fossiliferous Deccan infratrappean (Lameta Formation) and intertrappean sites, the Bagh Group of sediments, and location of the Raghavapuram Mudstone.](image-url)
(Khosla et al., 2003). Recent field prospecting in the Cretaceous sequences of the lower Narmada valley has led to the discovery of isolated archosaur teeth from an oyster-bearing green sandstone bed occurring at the top of the Coralline Limestone (Coniacian) from a site near Phutibawri village, Dhar District, Madhya Pradesh (Fig. 3). Of the three teeth recovered from this horizon, two are identified with abelisaurid dinosaurs and the third one with an indeterminate crocodile (Prasad et al., 2016). These fossils, conforming to the premaxillary and maxillary tooth morphology of Majungasaurus and Indosuchus, pre-date the earlier abelisaurid dinosaur reports from the Upper Cretaceous (Maastrichtian) Lameta Formation of Jabalpur, Pisdura (Central India) and Balasinor (Western India) and the Upper Cretaceous (Maastrichtian) Kallamedu Formation (South India). The same green sandstone bed at the top of the youngest geological unit (the Coralline Limestone) of the Bagh Group also yielded an elasmobranch fauna comprising Psychodus sp., Scapanorhynchus sp. aff. S. raphidon Agassiz, 1844, Cretodus sp. aff. C. crassidens (Dixon, 1850), Cretalumna sp., Squalicorax sp. aff. S. falcatus Agassiz, 1843, and Elasmostrachinoid indet. (Prasad et al., 2017b). This assemblage, previously widely documented from the Cretaceous deposits of North America, western Europe, North and West Africa, Far East and Near East from the Tethys belt, demonstrates that there was a clear change in elasmobranch faunal composition of India from cool temperate water forms in the early Late Cretaceous to essentially subtropical to tropical forms tracking the changing position of India during its northward drift.

**Cauvery Basin**

As the northward drift of India continued, sediments of the Trichinopoly and Ariyalur groups were deposited in the Ariyalur sub-basin of the Cauvery basin. Yadagiri and Ayyasami (1979) reported a partial skull and postcranial skeleton, attributed to a stegosaur Dravidosaurus blanfordi, from the Coniacian Anapaedi Formation of the Trichinopoly Group from a site near Siranattam village (Fig. 2). Latter examination of these bones led others to doubt its identification (Chatterjee and Rudra, 1996; Wilson et al., 2011), or regard it as nomen dubium (Maidment et al., 2008) or ?Stegosauria indet. (Pereda-Suberbiola et al., 2015).

Vertebrate fossils have been recovered at three levels within the Maastrichtian interval. A sauropod dinosaur egg belonging to Megaloolithus cylindricus (Ariyalur Group), originally known from the Upper Cretaceous Lameta Formation of Central India, was described from the shallow marine Upper Cretaceous (Lower Maastrichtian) Kallankuruchchi Formation (Fig. 2) (Kohring et al., 1996). More recently, Dhiman et al. (2017) reported sauropod dinosaur eggshell fragments representing Fusioolithus baghensis (Fernández and Khosla, 2015) from the shallow marine lower part of the Upper Cretaceous (Upper Maastrichtian) Kallamedu Formation (= Ottakovil Formation of Sastry et al., 1977) (Fig. 2). Eggshells with microstructure similar to that of M. cylindricus have been described from the Upper Cretaceous rocks of France and Upper Cretaceous Allen Formation of Argentina (Fernández and Khosla, 2015). Megaloolithus pseudomammilare from the Upper Maastrichtian deposits of Aix-en-Provence, France and Trevp Basin, Spain and Patagoolithus saltriades from the Upper Cretaceous of Salitral Moreno, Argentina were also considered as junior synonyms of F. baghensis (Fernández and Khosla, 2015). Hence this sauropod oospecies demonstrate close palaeobiogeographic links with both Southern Hemisphere continents and southern Europe.

The upper continental part of the Kallamedu Formation (Fig. 2) is long known for its fragmentary dinosaur bones (Blanford, 1862; Matley, 1929). Large limb and girdle bones comparable to those of titanosaurid sauropods of the Lameta Formation of Central India were identified in the fossil bones from the Kallamedu Formation (Matley, 1929). Yadagiri and Ayyasami (1979) reported bones of theropod, sauropod, and stegosaur dinosaurs from the Kallamedu Formation and described some of them as representing a new theropod dinosaur *Bruchathayosaurus matleyi*. According to Galton and Ayyasami (2017), the bones of *B. matleyi* do not exist any more as they disintegrated in the plaster jackets before reaching Geological Survey of India headquaters and *B. matleyi* is now regarded either as nomen dubium or Sauropoda indet. (Upchurch et al., 2004; Krause et al., 2006; Hone et al., 2016). Following a detailed study of supposed ornithischian dinosaur bone identified as a stegosaur dermal plate from the Upper Cretaceous Kallamedu Formation (Anonymous, 1978), Galton and Ayyasami (2017) concluded that this bone probably belongs to a sauropod. The Kallamedu Formation yielded remains of fishes: Lepisosteidae indet., *Egertonia* sp. (Prasad et al., 2013; Halliday et al., 2016); amphibian: Anura indet. (Prasad et al., 2013); turtle: *Kurmademys kallamedensis* (Gaffney et al., 2001); crocodiles: cf. *Simosuchus* sp., *Crocodylia* indet. (Prasad et al., 2013); dinosaurs: Abelisauridae indet. (Prasad et al., 2013), Troodontidae indet. (Goswami et al., 2013); and mammals: Sudamericidae indet. (Goswami et al., 2012). An isolated theropod tooth described from the Kallamedu site as *Megasaurus* sp. by Lydekker (1879) may actually belong to the abelisaurid dinosaurs.

The Kallamedu fauna thus has clades that have pan-Gondwanan affinities (gondwanatherian mammals and abelisaurid dinosaurs) (Goswami et al., 2012; Prasad et al., 2013) or Madagascar affinities (*Egertonia* sp., *Kurmademys*, simosuchid crocodyliform) (Gaffney et al., 2001; Prasad et al., 2013; Halliday et al., 2016) on one hand and a clade of Laurasian affinity such as troodontid theropod dinosaur (Goswami et al., 2013) on the other hand. Halliday et al. (2017) comparing fauna of all the Late Cretaceous localities of India and Madagascar demonstrated that the faunal composition of the Kallamedu Formation is distinct from that of the Deccan infra- and intertrappean beds, rather it shows greater faunal similarity with the Upper Cretaceous Maevarano Formation of Madagascar, despite the fact that the two landmasses were separated several million years ago.

**Deccan Volcanic Province**

During the late drift phase, the Indian plate passed over the Réunion hot plume which resulted in the eruption of Deccan flood basalts and splitting of the Seychelles from the Indian landmass. The Deccan Traps extruded in three major pulses interspersed with quiescent periods of considerable time; 1) phase I (~ 6% volume) occurred close to the base of C30n at ca. 67.4 Ma within the Maastrichtian, 2) phase II (~80% volume) erupted within C29r close to the Cretaceous-Palaeogene transition over a short period of time ranging from thousands to tens of thousands of years, 3) phase III (~14% volume) eruption took place at or near the base of C29n within the early Danian (Chenet et al., 2007, 2008, 2009; Jay and Widdowson, 2008; Jay et al., 2009; Schoene et al., 2015). Currently, the Deccan basalts occur in four major geographical provinces of peninsular India, viz., Main Deccan Volcanic Province, Mandla Lobe, Saurashtra, and
Malwa Plateau (Fig. 3). The Upper Cretaceous Lameta Formation (underlying the oldest basalt flow) and the sedimentary beds occurring intercalated with the Deccan lava flows (= intertrappean beds) have been an important source of vertebrate fossils representing the late drift phase of India. These Maastrichtian strata associated with the Deccan volcanic province (DVP) are the most intensively sampled Cretaceous rocks in India. A diversified vertebrate assemblage comprising all major groups of vertebrates except birds have been reported from the infra- and intertrappean beds (refer to Prasad, 2012 for the faunal list). This fauna consists of mixed Gondwanan and Laurasian clades.

**Taxa of Gondwanan affinity**

The Gondwanan clades are represented by amphibians: *Indobatrachus pusillus* (Myobatrachidae), Leptodactylidae indet., Hemisotidae indet., Hylidae indet., Ranoinidae indet.; snakes: *Indobatrachus sahni*, *Madtsosa pisidensis*, *Sanajeh indicus* (Madtsosauridae), *Comioophis* sp. (Aniliidae), turtles: *Carteremys leithii*, *Carteremys pisidensis*, Podocnemididae indet., *Sankuchemys sethna*, Bothremyidae indet., *Taphrosurus* spp.; dinosaurs: *Jainosaurus septentrionalis*, *Issiurus colberti*, *Hypselosaurus* sp., *Titanosaurusformes* indet. (sauropods), *Indosuchus raptorius*, *Indosaurus matteyi*, *Rajasaurus narmadensis*, *Lametasaurus indicus*, *Laevisuchus indicus*, *Rahiolisaurus gujaratensis* (abelisaurid theropods); mammals: *Bharaththerium bonapartei*, *Avashishta bacharamensis* (see Prasad, 2012 for references). The myobatrachid (*Indobatrachus*), leptodactylid, ranoid and hyloid amphibians are known from South America and Africa and are thus considered Gondwanan clades (Prasad and Rage, 1995, 2004). Prasad and de Lapparent de Broin (2002) had shown that isolated crocodilian teeth from the Deccan intertrappean beds appear to be morphologically similar to those of ziphodont crocodiles such as *Hamadasuchus* from the Early Cretaceous of Africa, and/or to *Mahajangasuchus* from the Late Cretaceous of Madagascar. The snake remains from the Deccan volcanic province assigned to nigoriphid *Indophis sahni* and madtsosaurids *Sanajeh indicus* and *Madtsosa pisidensis*, and Madtsosauridae indet. (Rage and Prasad, 1992; Rage et al., 2004; Wilson et al., 2010; Mohabey et al., 2011) are Gondwanan snakes with known fossil records from the Cretaceous of South America, Madagascar, Africa and India. The Indian abelisaurid dinosaurs (such as *Indosuchus*, *Laevisuchus*, *Lametasaurus*, *Rajasaurus*, *Rahiolisaurus*) show phylogenetic affinities with Late Cretaceous *Majungasaurus* and *Carnotauros* of Madagascar and South America, respectively (Wilson et al., 2003; Novas et al., 2010), whereas, the Indian dinosaur ootaxa show close resemblance to forms known from France, Spain, Africa and Argentina (Fernández and Khosla, 2015; Dhiman et al., 2018). In a review of parataxonomy of Late Cretaceous sauropod egg species of India and Argentina, Fernández and Khosla (2015) observed that five ooeuspic species, viz., *Megaloolithus jabalpurensis*, *M. cylindricus*, *M. megadermus*, *Fusosoolithus baghensis*, and *F. berthei*, are common to India, Argentina, Africa and southern Europe. According to them, a close phylogenetic relationship exists between the ooeuspic species of India and southern Europe, and between Patagonia (Argentina), India and Africa. Gondwanatherian (Sudamericidae) mammals were first documented from the Campanian of South America and were considered endemic to this continent. Later, they were documented from the Maastrichtian of India and Madagascar and the Eocene of Antarctica (Scillato-Yané and Pascual, 1984; Bonaparte, 1986; Krause et al., 1997) which implies that they had pan-Gondwanan distribution. Doubtful sudamericid mammals are also known from the Upper Cretaceous rocks of Tanzania (Krause et al., 2003). The haramiyidan mammals, though considered a Laurasian group since its oldest reports are known from the Late Triassic to Middle Jurassic of Europe and North America, have also been documented from the Late Jurassic of Tanzania and Early Cretaceous of Morocco and thus considered as relict forms of a formerly widely distributed group (Sigogneau-Russell, 1991; Heinrich, 1999; Hahn and Hahn, 2003).

**Taxa of Laurasian affinity**

The Laurasian clades include anurans: Pelobatidae indet., Costata incertae sedis, Gobiatiinae indet.; lizards: Anguidae gen. et sp. indet., dinosaurs: Troodontidae indet., and mammals: *Kharmerungulatum vanvaleni*. The pelobatid, Gobiatiinae and Costata frogs and Anguidae lizards had Laurasian origin and did not arrive in Gondwanan continents prior to early Palaeogene except India where they occur in the Upper Cretaceous intertrappean beds (Prasad and Rage, 1991, 1995, 2004; Rage et al., in press). *Kharmerungulatum* is morphologically similar to archaic ungulates *Protungulatum* and *Baiocodon* of North America (Prasad et al., 2007b). As a diverse assemblage of zebelastid mammals, possibly representing the ancestral stock for archaic ungulates of North America, has been documented from 85 Ma old rocks of West Asia (Archibald, 1996), *Kharmerungulatum* was interpreted as an immigrant from Laurasia. The troodontid theropod dinosaur reported from the Kallamedu Formation is the only report of this essentially Laurasian group from the Gondwana.

**Indian subcontinent as a centre of origin/ out-of-India dispersals**

It is assumed that following the split from Madagascar, the Indian plate served as a ‘biotic ferry’ carrying the Gondwanan lineages in isolation and offloaded the constituent biota on coming into contact with the Asian mainland. This was designated as “out-of-India” dispersal hypothesis (Krause and Maas, 1990; Bossuyt and Milinkovich, 2001). Bossuyt and Milinkovich’s (2001) hypothesis was based on molecular phylogeny of modern ranid frogs and over the years, it received further support from similar studies, such as that of cichlid and aplocheiloid fishes, ratite and passerine birds, caecilian amphibians, acrodont lizards, and Crypteroniaceae and Melastomataceae plants (Macey et al., 2000; Bossuyt and Milinkovich, 2001; Cooper et al., 2001; Gower et al., 2002; Conti et al., 2002; Sparks, 2004; Bossuyt et al., 2006). Likewise, floral remains recorded from the DVP such as Poaceae, and nonmarine diatoms (Ambwani et al., 2003; Prasad et al., 2005, 2011) have also lent support to out-of-India dispersal hypothesis.

Evidence for biotic endemity on the Indian plate, which remained physically isolated from other landmasses for about 35 Ma has been garnered from both living and fossil taxa. Molecular phylogeny of the extant frog *Nasikabatrachus sahyadrensis* (Nasikabatrachidae) from the Western Ghats has revealed Jurassic ancestry for this anuran family and since then it remained endemic to India (Biju and Bossuyt, 2003). Likewise, the caecilian amphibian family Chikilidae from northeast India diverged from the African family Herpelidae about 140 ± 20 m.y. ago and remained endemic to
this part of India (Kamei et al., 2012). Recent detailed study of turtle remains (mainly postcranial bones) from the intertrappean beds of Upparhatti, southwestern part of DVP revealed that the Indian Late Cretaceous turtles appear to be endemic at the generic level when precisely identified (de Lapparent de Braon and Prasad, in press) and share only plesiomorphic or homoplastic characters with Late Cretaceous bothremydid turtles of Gondwana. In fact, a high diversity of endemic species has been recorded among the ostracods. More than 100 species of ostracods have been reported so far from the Deccan intertrappean beds, of which 98% species were regarded as endemic to India (Whatley and Bajpai, 2006). In view of their oldest occurrences and high diversity in the Late Cretaceous of India, Whatley (2012) favoured Indian origin and out-of-India dispersal for Gomphocythere, Cypriodopsis and Eucypris.

In addition to these, adapisoriculid mammals documented from the Upper Cretaceous Deccan intertrappean beds (currently represented by Deccanolestes hislopi, D. robustus, D. narmadensis and Sahnitherium rangapurensis (Prasad and Sahni, 1988; Prasad et al., 1994, 2010; Rana and Wilson, 2003; Goswami et al., 2011)) are the only confirmed eutherian mammals known from the Cretaceous of Gondwana. The Indian adapisoriculid mammals are the most primitive with relatively high diversity. Derived forms appear in younger horizons (Palaeocene- Eocene) of NW Africa (Afrodon) and Europe (Afrodon, Blystylus). It is thus inferred that India was the centre of origin for adapisoriculid mammals in the Late Cretaceous and their dispersal to Africa and Europe took place close to the Cretaceous-Palaeogene (K/Pg) boundary (Prasad et al., 2010; Smith et al., 2010; Goswami et al., 2011). Additionally, the discovery of oldest fossil fruits of the vine family Vitaceae (Indovitis chitaleyae Manchester et al., 2013) in the Deccan intertrappean beds of Central India support an Indian origin for this group and out-of-India dispersal to Laurasia in the Palaeocene-Eocene times. Recently, Baas et al. (2017) reported oldest remains of eudicot plant wood belonging to the family Connaraceae (Connaroxyylon dimorphum) from the Deccan intertrappean beds and inferred an Indian origin and out-of-India dispersal for this family.

The out-of-India dispersal hypothesis implies that only one way dispersal from India to Asia was possible following the collision between these two landmasses. However, Yuan et al. (2018) have shown that Natatanuran frogs with African origins had dispersed to Asia between ~75.6 and 72.8 Ma using a terrestrial route (India as a ‘stepping stone’). In the reverse direction, the mantellid frogs of Asian ancestry had possibly dispersed to Madagascar close to K/Pg boundary possibly using the same land connection (Van der Meijden et al., 2007; Kurabayashi et al., 2008).

### India-Madagascar biogeographic link

Considering the more recent (~88 Ma) separation of Madagascar from India, the biogeographic affinities between these landmasses must be expected to be closely related to each other. Study of Amniote remains (mainly postcranial bones) from the intertrappean beds of Upparhatti, southwestern part of DVP revealed that the Indian Late Cretaceous turtles appear to be endemic at the generic level when precisely identified (de Lapparent de Braon and Prasad, in press). The presence of closely related taxa may be attributed to former wide spread distribution of the ancestral stocks in the Gondwana before its break-up and the Late Cretaceous similarities are the result of retention of primitive morphological traits in the descendants (Ali and Krause, 2011) or alternatively they reflect the more recent biogeographic connections between these landmasses.

Close phylogenetic relationships have been established between nigeropheid snake Indophis fanamhina (Pritchard et al., 2014), madtsoiid snake Madtsoia madagascarensis, bothremydid turtle Kinkonychelys hechti (Gaffney et al., 2009), and gondwanatherian mammal Lavanify miolaka (Krause et al., 1997) of Madagascar and Indophis sahni (Rage and Prasad, 1992), Madtsoia pisuredens (Mohabey et al., 2011), Kurmademys kallamedensis (Gaffney et al., 2001), and Bharathierium bonapartei (Prasad et al., 2007a) of India, respectively. The phylolepid fish Egeronia and Simosuchus-like crocodyliform reported from the Kallamedu Formation, India are the only known reports of these taxa outside Madagascar (Prasad et al., 2013; Halliday et al., 2016). Based on these faunal similarities, we subscribe to the view that faunal dispersal routes existed in the Late Cretaceous between India, Madagascar, Africa and Europe. This view receives further support from the recent phylogenetic study of Arcovenator, an abelisaurid dinosaur from the Late Cretaceous of France. Tortosa et al. (2014), while discussing the phylogenetic relationships of this large-bodied Late Campanian abelisaurid, posited that a close phylogenetic relationship exists between Arcovenator and Maastrichtian abelisaurids from India (Rajasaurus, Indosaurus, Rahiollisaurus) and Madagascar (Majungasaurus) rather than with small-bodied European abelisaurids, and nested them within the subfamily Majungasaurina. This implies that these taxa had a geographically closer common ancestor than other Gondwanan abelisaurids such as brachyrostyans of South America. According to Tortosa et al. (2014), dispersal of Majungasaurinae abelisaurids between the Indian subcontinent, Madagascar and Europe via Africa was possible through some terrestrial links. A similar dispersal route has been favoured for Sabalites dindoriensis, a coryphoid palm of Laurasian origin, present in the Upper Cretaceous intertrappean beds of Central India (Srivastava et al., 2014).

### Potential modes of faunal exchanges

One of the greatest biogeographic conundrums of India’s drift history is its biological connectivity with adjacent continents. Palaeogeographic maps depict the Indian plate as an island fully isolated from other landmasses following its separation from Madagascar around 88 Ma until its collision with the Asian mainland at about 55 Ma. This implies that India was a ‘Noah’s Ark’ or a ‘Biotic Ferry’ during its Late Cretaceous drift without any physical connection with other landmasses and may have developed endemic biota which later dispersed into Asia following its collision with the latter. Contrary to the long held view that faunal interchanges could take place between these landmasses only after collision between India and Asia, Sahni (1984) suggested that the Late Cretaceous biota of the Deccan volcanic province is cosmopolitan in nature with close affinities to Gondwanan and Laurasian faunas. He speculated on the presence of possible filter corridors between Africa and India through the Mascarene Plateau and Chagos-Laccadive Ridge that facilitated biotic dispersals during the Late Cretaceous. In view of the biotic similarities between South America, India and Madagascar, and India and Laurasia, it was debated whether the biotic dispersal routes were either northern or southern land bridges/landspans or stepping-stones, such as island-arcs, oceanic islands or microcontinents that facilitated faunal and floral dispersals into and out of India during its rapid drifting phase (Briggs, 1989, 2003; Krause et al., 1997; Rage, 1996, 2003; Prasad and Sahni, 1999, 2009; Ali and Aitchison, 2009; Prasad et al., 2010; Chatterjee et al., 2013, 2017).
In order to explain similar faunas in India, Madagascar, and South America, Krause et al. (1997) envisaged a terrestrial connection between South America and India–Madagascar via Antarctica and Kerguelen Plateau (Krause et al., 1997; Hay et al., 1999) in the Late Cretaceous, whereas Case (2002) argued that Antarctica and Madagascar were linked by the Gunnerus Ridge during the mid-Late Cretaceous rather than through Kerguelen Plateau (Fig. 4). Ali and Aitchison (2009) have shown that these southern land bridges were submerged by the end of Early Cretaceous (~115 Ma) and deep water gaps developed between northward moving Indo-Madagascar block and Antarctica inhibiting any faunal interchanges. Ali and Krause (2011), while rejecting the southern connection between South America and Indo-Madagascar-Seychelles block around 88 million years ago through Kerguelen Plateau or Gunnerus Ridge, suggested that many Late Cretaceous taxa of South America, India and Madagascar may represent relictual lineages that evolved vicariantly from their ancestral stocks somewhere in Gondwana during the Early and “middle” Cretaceous time.

To explain the presence of faunas with Laurasian affinities within the intertrappean beds an early India/Asia collision at the K/Pg boundary was proposed by Jaeger et al. (1989) (Fig. 5A). However, geophysical data and sedimentary record at the northern margin of India do not support this hypothesis (Prasad and Sahni, 1999). Prasad and Sahni (1999, 2009), on the other hand, postulated that the faunal exchange between India and Asia prior to their collision occurred through sweepstakes dispersals across the Tethys Sea (Fig. 5D, Fig. 6). According to them, the Trans Himalayan Arc, Kohistan and Dras island arcs and oceanic islands that were consumed at the subduction zone may have served as ‘stepping stones’ for faunal dispersals. To strengthen their argument they pointed out that the faunal elements involved in such an exchange were small-sized tetrapods such as pelobatid, Gobiatidae, and Costata anurans, Anguidae lizards, and charophytes. However, the report of a troodontid dinosaur, an essentially Laurasian group, from the Upper Cretaceous Kallamedu Formation of Cauvery Basin does indicate that even large animals were involved in the faunal exchange with Laurasia unless troodontids are proved to be Pangaean in distribution. Existence of shallow trans-Tethyan connection between India and Eurasia in the Late Cretaceous was envisaged on the basis of common occurrence of Igdabatis indicus Prasad and Cappetta, 1993 in India and Spain (Soler-Gijón and López-Martínez, 1998). Briggs (1989, 2003) suggested that close proximity of Greater India to Africa and Eurasia in the Late Cretaceous enabled free faunal interchanges between these landmasses (Fig. 5 B). Chatterjee and Scotese (1999), on the other hand, opined that the Late Cretaceous terrestrial link between Greater India and Greater Somalia accounts for the common occurrence of Gondwanan and Laurasian elements in the Late Cretaceous vertebrate fauna of India (Fig. 5C). Later Chatterjee and colleagues proposed a dispersal route between India and Africa via Oman-Kohistan-Ladakh Arc, a variant of Prasad and Sahni’s (1999, 2009) island arc dispersal model, instead of biological connectivity through Greater Somalia (Chatterjee and Scotese, 2010, Chatterjee et al. 2013).

The sister group relationships of various Late Cretaceous vertebrate taxa of India and Madagascar even after >20 Ma separation demands a sound explanation. Patriat and Segoufin (1988) had suggested a Late Cretaceous connection between Madagascar and India across the Seychelles Plateau and volcanic islands through which transoceanic dispersal were possible, a hypothesis supported later by Rage (1996). Using faunal similarity network analyses, Halliday et al. (2017) demonstrated close Late Cretaceous faunal similarities between India and Madagascar and suggested trans-oceanic dispersal of terrestrial and freshwater taxa between the two landmasses across a series of islands. While debunking the southern Kerguelen Plateau terrestrial route, Ali and Aitchison (2008) felt that the only possible link between India and Africa was through the Seychelles, Amirante Ridge, Providence Bank and Madagascar. Earlier, Averianov et al. (2003) reinterpreted the supposed marsupial tooth from the Late Cretaceous of Madagascar (Krause, 2001) as a zhelestid eutherian.
Figure 5. Palaeogeographic models proposed in the past to explain the occurrence of Gondwanan and Laurasian biotic elements in the Late Cretaceous deposits of India. A. Early India/Asia collision at the K/Pg boundary proposed by Jaeger et al. (1989). B. Greater India located close to Eurasia and northeastern Africa with its southern tip placed adjacent to the northern tip of Madagascar (Briggs, 2003). C. Greater India-Somalia terrestrial connection as suggested by Chatterjee and Scotese (1999). D. Dispersals across island arcs as proposed by Prasad and Sahni (1999, 2009). E. Rage’s (2003) palaeogeographic model suggesting a continuous terrestrial connection between Eurasia and Madagascar through India and the Seychelles Plateau.
similar to Maastrichtian *Lainodon* (Gheerbrant and Astibia, 1999) from Spain and supported a terrestrial connection between Europe and Madagascar in the Late Cretaceous via Africa. An end Cretaceous terrestrial connection between Madagascar and Laurasia via India and the Seychelles Plateau was also envisaged on the basis of past and present distribution of iguanid lizards and boine snakes (Rage, 1996, 2003). In their review on the Mesozoic biogeographic history of Madagascar, Krause et al. (2019) also commented that some Late Cretaceous connections existed between Madagascar, India, Africa and Eurasia though the tectonic elements that made these connections possible are unknown at present. More recently, Torsvik et al. (2013) recognised a supposed microcontinent Mauritia and speculated on possible presence of a number of Precambrian microcontinental fragments in the Indian Ocean between Madagascar and India which are now concealed by the volcanic islands that track the northward drift of the Indian plate as it passed over the Réunion hotspot. The Laxmi Ridge, which lies to the north of the Seychelles microcontinent and buried beneath thick Indus Fan sediments, has been considered as a continental sliver isolated during the Seychelles/India break-up (Bhattacharya et al., 1994; Collier et al., 2004). Prior to their burial by the oceanic basalts, these microcontinents along with the Seychelles Plateau, Amirante Ridge, Providence Bank may have formed important stepping stones between India and Madagascar allowing faunal interchanges between them (Fig. 6). On the other hand, the island arc systems and oceanic islands to the north of Greater India might have facilitated direct dispersal from the north or through Africa in the northwest (Fig. 6).

Yuan et al. (2018) using molecular phylogenies and divergence time estimates of Natatanura frogs of Madagascar also support the Indian plate as a ‘Stepping Stone’ for dispersals between Africa, Madagascar and Asia. They identify four time slices (between 130-88 Ma, 88-55 Ma, 55-25 Ma, 25-0 Ma) during which land bridges existed between these landmasses. According to this study, the first dispersal of Natatanuran frogs from its most common recent ancestor inhabiting Africa to India occurred at about 72 Ma, leading to the development of two endemic Indian families Ranixalidae and Micrixalidae. The endemic Madagascan Mantellidae with an Asian ancestry dispersed from Asia to Madagascar using India as a ‘stepping stone’ around 62.4 Ma ago. More recently, Garg and Biju (2019) showed that, the endemic microhylid frogs from the Western Ghats having affinities with Southeast Asian forms used two land bridges, one at about ~45.1 Ma and the second one around ~39.7 Ma, to colonize Southeast Asia. These dispersal events, interspersed with brief period of isolation, testify to periodic faunal interchanges between India and Asia prior to and during the suturing of these two landmasses. On the whole, the extant and fossil tetrapod fauna from the Upper Cretaceous deposits of India indicate close biogeographic connections between the Indian subcontinent, Madagascar, and Eurasia at a time when the former was suggested to be physically isolated from other landmasses.

**Summary**

Close examination of the Cretaceous vertebrate fauna reveal a complex biogeographic history for the Indian plate. The early-drift phase (i.e. Early Cretaceous) vertebrate fossil record of the Indian plate is poorly understood at present, but the limited data from the Karai Formation demonstrates a high latitude placement of the Indian plate. However, by the Campanian time, the vertebrate fauna becomes fully adapted to tropical to subtropical climate of the Tethyan realm. The better documented late-drift phase (i.e. Late Cretaceous) fossil record of India coming from the DVP and the Kallamedu Formation of the Cauvery Basin offers a wide range of biogeographic scenarios. Fossils from both DVP and the Cauvery Basin contain clades of both Gondwanan and Laurasian affinities. In addition to these, some endemic taxa that originated and evolved during India’s long physical isolation and later dispersed out of India also co-existed. However, the fauna of Cauvery Basin is significantly different from the DVP fauna. The Upper Cretaceous Kallamedu fauna is taxonomically more similar to Madagascan forms despite the fact that geophysical data shows >20 Ma isolation of India from Madagascar following their break-up. The presence of various vertebrates showing Gondwanan and Laurasian affinities have been explained by different southern
and northern dispersal models. Though a southern terrestrial route across Kerguelen Plateau and Antarctica was proposed in the past to explain the presence of taxa of Gondwanan affinities, it is found to be no more valid. Instead, the close phylogenetic relationships between the Late Cretaceous vertebrate clades of India and Madagascar favours land connections between these areas through the Seychelles, Amirante Ridge, Providence Bank and supposed currently buried microcontinental fragments. On the other hand, it is suggested that Laurasian elements of Indian Late Cretaceous vertebrate fauna used island-arc systems and oceanic islands to the north of Greater India as stepping stones to reach India directly or via Africa. In addition to this mode of dispersal, long distance rafting may have also played a significant role in the dispersal of small-sized animals between these landmasses. In the Late Cretaceous, Indian plate thus served as a stepping stone for the southern Gondwanan taxa to disperse out-of-India and the northern Laurasian taxa to reach Madagascar.

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