

Cretaceous insular India – Consequences for biological evolution and faunal interchanges

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India underwent a significant length of northward journey after its break-up from the contiguous landmasses of Gondwana and remained for a large part of the time, particularly during the Cretaceous Period, physically isolated from other landmasses. The consequences of a long period of isolation for constituent biological communities are evaluated in this review by examining the Late Cretaceous fossil biota of India. The fossil record from the Upper Cretaceous Lameta Formation, Deccan intertrappean beds, and the Kallamedu Formation bring forth fauna and flora that are considered to have taxonomic affinities either to those of Gondwana or Laurasia or had origins in the northward drifting Indian plate. During the present analysis, it is inferred that the fauna of Gondwana affinity confirms a vicariant biogeographic scenario with many of the taxa having sister group relationships with those of Madagascar. Several taxa, such as adapisoricolid mammals, bothremydid turtles, ostracods, and at least five plant groups were endemic to India and made their way to Laurasia following India/Asia collision thus supporting out of India dispersal hypothesis. The taxa of Laurasian lineages are interpreted to have dispersed into India using Kohistan–Dras–Oman island arcs as steppingstones, facilitated by a sweepstakes mode of dispersal.

Keywords: Cretaceous, Deccan, Lameta Formation, Intertrappean, Kallamedu Formation, Drifting India

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INTRODUCTION

The Indian subcontinent has a unique geodynamic history of being part of the Gondwana supercontinent, later rifting from contiguous Gondwanan landmasses and drifting northwards in isolation until its collision with Asia. The major rifting and drifting events occurred in the Cretaceous. For example, in the Early Cretaceous (~130-120 Ma ago) India's land connections were severed from other East Gondwana landmasses (Australia and Antarctica), and in the Late Cretaceous India broke away from Madagascar (~90 Ma ago) and Seychelles (~65 Ma ago). The latter event coincided with the Deccan volcanism, one of the largest continental flood basalt eruptions on the Earth, which has been considered one of the causes of the mass extinction at the Cretaceous-Palaeogene boundary (McLean, 1985; Keller *et al.*, 2012). During this long journey from south to north, India passed through different palaeolatitudes and palaeoclimatic zones (Powell, 1979; Chatterjee *et al.*, 2013). Disjunction of once contiguous landmasses may lead to vicariant evolution of pre-existing faunal and floral groups and ultimately result in the development of endemic faunas as is evident from the Cretaceous continental biotas of South America and Madagascar. Did the Indian subcontinent which remained insular for a long duration of geological time (~30-

35 Ma) host endemic biota as is the case with South America and Madagascar? Or were there some intermittent biotic interchanges between insular India and other landmasses? Continental biotas are best suited to throw light on the pattern of evolution and dispersals of fauna and flora during the physical isolation of a landmass as the ocean forms an important barrier for the dispersal of terrestrial biota and therefore may lead to the development of endemic fauna and flora. To understand the evolution of Cretaceous biota in insular India, a critical examination of the fossils from continental Cretaceous sedimentary deposits of peninsular India is crucial. Fossiliferous continental Cretaceous deposits of India are broadly represented by the Lower Cretaceous Gangapur Formation of Pranhita–Godavari valley, the Upper Cretaceous Lameta Formation (= infratrappean, referring to its stratigraphic position below the Deccan volcanic flows), the Upper Cretaceous (and a few Lower Palaeocene) Deccan intertrappean beds (Fig. 1) (referring to their stratigraphic position between the Deccan lava flows), and Upper Cretaceous (Late Maastrichtian) Kallamedu Formation of the Cauvery Basin, South India. This synoptic essay relies heavily on the fossil record documented in the last three decades from these fossiliferous Cretaceous deposits of peninsular India.

The fossil record from the Lower Cretaceous Gangapur Formation is currently limited to a few vertebrate taxa (Prasad *et al.*, 2004) and a considerable number of plant fossils and

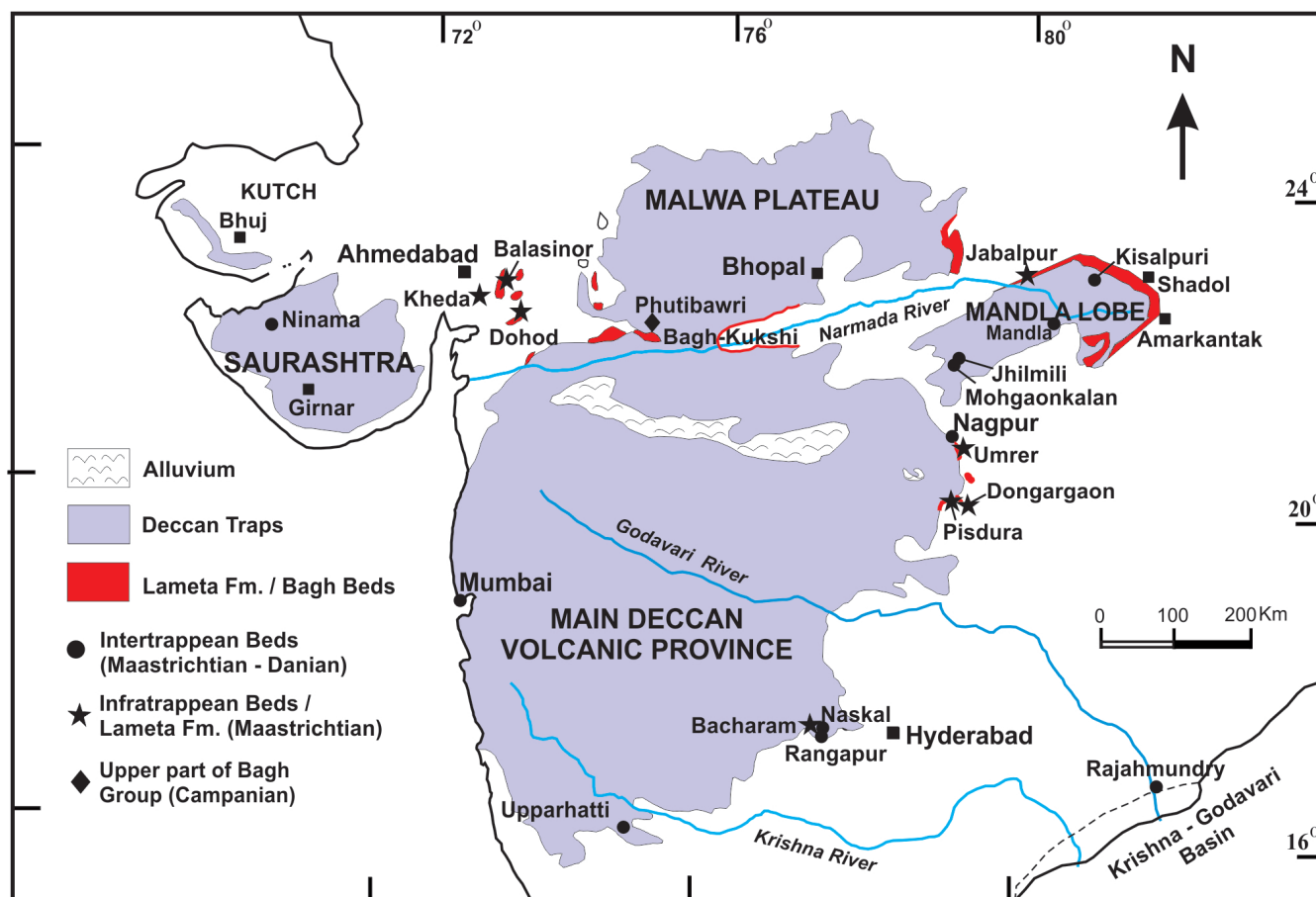


Fig. 1. Map of peninsular India showing the distribution of pre-Lameta, Lameta and intertrappean fossil sites discussed in the paper.

does not throw much light on India's Early Cretaceous biogeographic history. However, it is worth mentioning here that marine shark fossils described from the Lower–Upper Cretaceous (Albian–Cenomanian) Karai Formation of the Cauvery Basin point to a high palaeolatitude position for India, as the majority of the species described are known only from antitropical high palaeolatitude areas of both the hemispheres (Underwood *et al.*, 2011). The bulk of the Cretaceous vertebrate fossils significant for the present discussion comes from the Lameta Formation, Deccan intertrappean beds, and the Kallamedu Formation.

Institutional Abbreviations: VPL/JU and VPL/JU/NKIM/ stand for Jammu University vertebrate fossil collections and Naskal Intertrappean Mammal collections, respectively; DUGF refers to Delhi University, Department of Geology fossil collections.

CRETACEOUS FOSSIL SITES AND CHRONOLOGY

Pre-Lameta fossil sites

The Bagh Group is divided into the Nimar Sandstone,

Nodular Limestone, and Coralline (=Bryozoan) Limestone formations are assigned Cenomanian, Turonian, and Coniacian ages, respectively (Jaitly and Ajane, 2013). The basal part of the Nimar Sandstone was considered to have been deposited in a fluvial–brackish environment, whereas the top of the Nimar Sandstone, the Nodular Limestone, and the Coralline Limestone were interpreted as shallow marine deposits (see Jaitly and Ajane, 2013). Khosla *et al.* (2003) described some partially preserved bones of titanosaurid dinosaurs from the Nimar Sandstone which represent the oldest known Cretaceous titanosaurid fossils from India.

A vertebrate fossil-bearing horizon was recognized in a green-coloured sandstone, at the top of the Coralline Limestone. This glauconite-bearing green sandstone was considered to represent the basal part of the Lameta Formation by Bajpai *et al.* (2013) whereas preliminary Ar^{40}/Ar^{39} dating of glauconite minerals from this sandstone indicated an age of ~75 Ma (pers. comm. Prof. Kanchan Pande), thus placing the green sandstone bed within the Campanian Stage. Recent works revealed the presence of shark teeth, crocodile, and abelisauroid dinosaur teeth in this green sandstone unit (Prasad *et al.*, 2016; 2017). If the Campanian age is confirmed for the green sandstone unit, the abelisauroid dinosaur teeth would represent the oldest record of this group from India. Further, it would have implications for its stratigraphic status vis-à-vis the Lameta Formation.

Lameta fossil sites

Most of the vertebrate body fossils from the Lameta Formation are derived from the type section in Jabalpur in the east and the sections in the west near Balasinor and Pisdura–Dongargaon–Nand basins in Central India (see Prasad, 2012; Prasad and Sahni, 2014 and references therein). In addition to these three geographic regions, extensive dinosaur nesting sites have also been documented from Bagh–Kukshi area in west-central India (Dhiman, 2021; Dhiman *et al.*, 2021). The Lameta Formation was assigned a Maastrichtian age based on the presence of *Ariadnaesporites* and *Aquilapollenites* palynofossils (Dogra *et al.*, 1988), dinosaurs (Buffetaut, 1987), a brackish to marine water myliobatid fish *Igdabatis* (Jain and Sahni, 1983), magnetostratigraphy that placed volcanic flows overlying the Lameta Formation (at Jabalpur) in magnetochron C30n (Courtilot *et al.*, 1986) and by $^{40}\text{Ar}/^{39}\text{Ar}$ radiometric dating of the basal volcanic flow (Courtilot *et al.*, 1988).

Jabalpur: Ever since the discovery of the first dinosaur fossils of India from the ‘Lameta Beds’ by the British army captain Sleeman in 1828 (Sleeman, 1844), dinosaur skeletal remains have been documented from the Lameta type section in Jabalpur (Huene and Matley, 1933; also see Carrano *et al.*, 2010 and Chatterjee, 2020). Titanosaurid dinosaur nesting sites in the Lameta Formation of Jabalpur, their taphonomy, and the depositional setting were also discussed comprehensively by Sahni *et al.* (1994). Hence, the Cretaceous dinosaur diversity of India is primarily known from this site. In addition to the large bones and eggs of dinosaurs, vertebrate microfossils represented by lepisosteid, osteoglossid, and myliobatid fishes, freshwater ostracods and charophytes have also been documented from the Lameta outcrops of Jabalpur (Courtilot *et al.*, 1986; Sahni and Tripathi, 1990; Khosla and Sahni, 2000; Khosla *et al.*, 2011; Khosla, 2014).

Pisdura–Dongargaon–Nand area: Vertebrate fossils belonging to bony fishes (*Lepisosteus indicus*, *Pycnodus lametae* and *Eoserranus hislopi*) were reported from the Lameta Formation of Dongargaon as early as in 1908 (Woodward, 1908). Subsequently, fish, turtle, and dinosaur (bones and coprolites) remains, ostracods, and molluscs were collected by Matley during his 1932–33 exploratory work (in Carrano *et al.*, 2010) from the Lameta outcrops of Pisdura and Warora. Jain (1977; 1986) described a skull and a partial carapace of pelomedusoid turtle (*Shweboemys pisdurensis*) from the Lameta Formation of Pisdura and Dongargaon, respectively. In a recent taxonomic revision of this turtle material, *Shweboemys pisdurensis* was placed in a new combination *Jainemys pisdurensis* with a referral to the clade Kurmademydini (Joyce and Bandyopadhyay, 2020). Later works by Jain and Sahni (1983; 1985), Mohabey *et al.* (1993), and Verma *et al.* (2017) have brought more fish taxa to our knowledge from Pisdura–Dongargaon area. Vertebrae belonging to the madtsoiid snake (*Madtsoia pisdurensis* Mohabey, Head and Wilson, 2011), remains of titanosaurid dinosaur (Wilson and Mohabey, 2006), ostracods (Khosla *et al.*, 2005; 2010), and palynomorphs (Samant and Mohabey, 2005) are the recent additions to the Lameta biota of this area. Another important finding from the Lameta beds of this area is the report of grass phytoliths from dinosaur coprolites (Prasad *et al.*, 2005). This has important implications for the

origin and evolution of grasses and dietary adaptations in early mammals such as gondwanatheres.

Balasinor area: Balasinor area in Kheda District in Gujarat hosting the westernmost exposures of the Lameta Formation has become famous for its dinosaur nesting sites. The first documentation of dinosaur eggs from this region was by Mohabey (1983). Later detailed microstructural studies of the dinosaur eggs from this area were undertaken by Srivastava *et al.* (1986) and Mohabey (1998), and nine oospecies of titanosaurid dinosaurs were described. Though no embryos were found in these eggs, based on the similarity of eggshell morphology to those identified as titanosaurid eggs from Argentina, the eggs from the Lameta Formation were assigned to titanosaurids (Sahni *et al.*, 1994; Khosla and Sahni, 1995; Mohabey, 1998). Besides the oological material, some disarticulated bones collected by the palaeontologists of the Geological Survey of India near Rahioli village were identified as those of abelisaurid dinosaur (a theropod clade from the southern continents) *Rajasaurus narmadensis* (Wilson *et al.*, 2003). After this find, a nearly complete postcranial skeleton collected by Sankar Chatterjee from Rahioli dinosaur excavation site was also identified as an abelisaurid dinosaur *Rahiolisaurus gujaratensis* by Novas *et al.* (2010). Chatterjee (2020) mentioned the presence of several skeletal remains such as vertebrae, scapulocoracoid, humerus, femur, and armor bones belonging to a possible nodosaurid ankylosaurid dinosaur from Rahioli. Another remarkable finding from the Lameta beds of Balasinor is the skeleton of a madtsoiid snake (*Sanajeh indicus*) which was found coiled around three titanosaurid dinosaur eggs and a skeleton of titanosaurid hatchling, as it was in the act of stealing the contents of eggs (Wilson *et al.*, 2010).

Bagh–Kukshi area: This area lies in between the type locality at Jabalpur in the east and the outcrops of Balasinor in the west. So far, no body fossils were reported from the Lameta outcrops of this area. Khosla and Sahni (1995) documented seven dinosaur oospecies from this area based on eggshell micro and ultrastructure. More recently extensive nesting sites have been identified in Bagh and Kukshi localities (Dhiman, 2021; Dhiman *et al.*, 2021).

The sauropod dinosaur skeletal remains collected from the Lameta outcrops of Jabalpur, Pisdura–Dongargaon, and Balasinor have been assigned to *Titanosaurus indicus*, *T. blanfordi*, *T. colberti*, *T. rahioliensis*, *Antarctosaurus septentrionalis*, *Laplataosaurus madagascarensis* in the past (Huene and Matley, 1933; Prasad and Verma, 1967; Mathur and Pant, 1986; Jain and Bandyopadhyay, 1997). Recent revisions reveal the presence of only three taxa viz., *Isisaurus (Titanosaurus) colberti*, *Jainosaurus (Antarctosaurus) septentrionalis* and *Titanosauriformes* indet. (Hunt *et al.*, 1994; Wilson and Upchurch, 2003; Wilson and Mohabey, 2006). Likewise, the theropods, *Indosuchus raptorius*, *Indosaurus matleyi*, *Ornithomimoides mobilis*, *O. (?) barasimlaensis*, *Dryptosauroides grandis*, *Coeluroides largus*, *Lametasaurus indicus*, *Laevisuchus indicus*, *Jubbulpuria tenuis*, and *Composuchus solus* (Matley, 1923; Huene and Matley, 1933) recognized from Jabalpur, following taxonomic revisions and recent reports from Balasinor, were assigned to *Indosuchus raptorius*, *Indosaurus matleyi*, *Laevisuchus indicus*, *Rajasaurus narmadensis*, and *Rahiolisaurus gujaratensis* (Wilson *et al.*, 2003; Novas *et al.*, 2004; 2010). All these taxa are referred to the clade Abelisauroida.

Though fourteen sauropod oospecies were documented from Balasinor (Mohabey, 1998) and Bagh-Kukshi (Khosla and Sahni, 1995), subsequent revisions (Vianey-Liaud *et al.*, 2003; Fernández and Khosla, 2015) consider *Megaloolithus cylindricus*, *M. jabalpurensis*, *M. megadermus*, *M. dhoridungriensis*, *M. khempurensis* (Megaloolithidae), *Fusioolithus mohabeyi*, *F. baghensis*, *F. dholiyaensis*, *F. padiyalensis* (Fusioolithidae) and *Ellipsoolithus khedaensis* (Elongatoolithidae) as the only valid taxa.

A special mention needs to be made here about Bacharam site located about 13 km west of Vikarabad town in Rangareddi District, Telangana where the sedimentary beds occur in an infratrappean stratigraphic position. This site assumes great significance from the point of early mammal evolution in Gondwana because of the documentation of the youngest haramiyid mammal (*Avashishta bacharamensis* Anantharaman, Wilson, Das Sarma and Clemens, 2006). This is also the first record of a Cretaceous mammal from the infratrappean sedimentary deposit of India.

Deccan intertrappean sites

The sedimentary units intercalated with the Deccan volcanic flows and commonly known as intertrappean beds occur all over the Deccan volcanic province (Fig. 1). These sedimentary deposits have been an important source of biota that lived during the rapid northward flight of India in isolation. The age assignments of the intertrappean beds are not based on unequivocal evidence. Firstly, the stratigraphic position of different intertrappean sections with respect to each other is not known as broadly correlatable flow stratigraphy is not available for the entire Deccan volcanic province. At present, no well-defined magnetostratigraphic framework or radiometric dates for the underlying and overlying basaltic flows is available for the studied intertrappean sections. Even if available, they may not be of great help as the duration of intertrappean sedimentation may be less than the error bars associated with the geochronological ages. As the intertrappean beds are dominantly freshwater-lacustrine deposits, no biostratigraphically significant taxa such as foraminifers are available for age estimates. Most of the age determinations are based on ostracods, myliobatid fish *Igdabatis*, palynofossils, and the presence of dinosaur remains. Freshwater ostracod fauna has been extensively reported from a large number of intertrappean outcrops (Whatley and Bajpai, 2006; Whatley, 2012; Kshetrimayum *et al.*, 2021) and generally used as evidence for Maastrichtian age (Bhatia *et al.*, 1996; Whatley and Bajpai, 2006). This evidence, however, appears to be unreliable as similar ostracod assemblage has also been documented from the well-dated Lower Palaeocene (Danian) Jhilmili intertrappean beds (Khosla *et al.*, 2009). A palynological assemblage consisting of *Aquillapollenites bengalensis* - *Gabonispuris vigourouxii* - *Azolla cretacea* is another line of evidence used for assigning a Maastrichtian age for the intertrappean beds (Sahni *et al.*, 1996). The myliobatid fish *Igdabatis* is one more fossil group often used for assigning a Maastrichtian age. The genus *Igdabatis* documented so far from the Maastrichtian of Niger (Cappetta, 1972) and Campanian of Spain (Soler-Gijón and López-Martínez, 1998; Kriwet *et al.*, 2007), is also known from Lameta and intertrappean beds (Jain and

Sahni, 1983; Courtillot *et al.*, 1986; Prasad and Cappetta, 1993; Lourembam *et al.*, 2017; Verma *et al.*, 2017) which are considered as Late Cretaceous based on palyno and dinosaur fossils. This genus has not been reported from stratigraphic levels older or younger to the Deccan infra- and inter-trappean beds. The Cretaceous age connotation to *Igdabatis* appears to be in good standing as no fossils morphologically similar to *Igdabatis* were documented from the Upper Palaeocene Fatehgarh Formation (Rana *et al.*, 2006). Likewise, the recently collected elasmobranch fauna from the Lower Palaeocene (Danian) Niniyur Formation though contains other myliobatids did not yield any *Igdabatis* specimens. Hence *Igdabatis* is considered here as a reasonably good indicator of Late Cretaceous age. Additionally, the presence of dinosaur remains further strengthens a late Cretaceous age for the intertrappean beds. Using these criteria, a majority of the Deccan intertrappean beds were interpreted as Maastrichtian in age. A few intertrappean beds are regarded as Early Palaeocene in age. From some of these beds, such as from the shallow marine – brackish water intertrappean outcrops of Rajahmundry and subsurface sections of the Krishna-Godavari basin (Raju *et al.*, 1991; Jaiprakash *et al.*, 1993; Keller *et al.*, 2012) and the intertrappean beds of Jhilmili in Central India (Keller *et al.*, 2009) age diagnostic Early Palaeocene (Danian) foraminifera were documented. The intertrappean beds of Ninama (Samant *et al.*, 2014) and Papro (Singh and Kar, 2002; Sharma and Khosla, 2009) were also dated Early Palaeocene based on palynofossils and ostracods, respectively. In the case of Papro, alternatively, a Maastrichtian age was suggested based on vertebrate microfossils (Shome and Chandel, 2013).

A vast amount of literature is available on a large number of fossiliferous intertrappean sections that have been studied in the recent past (refer to Khosla and Sahni, 2003; Prasad, 2012; Khosla and Verma, 2015; Kapur and Khosla 2016; Verma *et al.*, 2017). For the context of the present paper, only the following intertrappean sites are discussed as they have preserved some taxa significant from the point of view of evolution and palaeobiogeography.

Naskal–Rangapur: The intertrappean beds of Naskal are located about 70 km west of Hyderabad and 2 km northeast of Naskal village in Rangareddi District, Telangana. This intertrappean site attracted the attention of the scientific community with the report of the first Cretaceous mammal from India (Prasad and Sahni, 1988). The Naskal intertrappean site has yielded the most diversified assemblage of vertebrates among all known fossiliferous Deccan intertrappean horizons with the record of fish, amphibians, lizards, snakes, crocodiles and mammals. Gastropods, ostracods, and charophytes were also found in association with the vertebrate fossils. Based on the similarity of fish fauna to other Cretaceous intertrappean beds such as Asifabad and Nagpur and palynofossils, the Naskal site was assigned the latest Cretaceous age (Prasad and Sahni, 1988; Prasad and Khajuria, 1990; Sahni *et al.*, 1996; Khajuria and Prasad, 1998; Singh *et al.*, 2006). This site also yielded, though rarely, teeth belonging to *Igdabatis*. The rarity of this taxon implies that the Naskal intertrappean beds were deposited in a lacustrine basin distal to a coastal plain (Prasad and Khajuria, 1996; Khajuria and Prasad, 1998). Recently, Wilson *et al.* (2022) suggested that the intertrappean beds of Naskal are the latest Cretaceous (66.136–66.056 Ma) in age based on geochemical correlation,

⁴⁰Ar/³⁹Ar dating, and magnetostratigraphy of underlying and overlying basaltic flows, and palynological study of the intertrappean sediments. This site is very important because it has yielded palaeobiogeographically significant Gobiatinae frogs, *Indophis sahnii* (Nigerophiidae) Rage and Prasad, 1992, Anguillidae lizards (Prasad and Rage, 1995), eutherian mammals (*Deccanolestes hislopi* Prasad and Sahni, 1988, *D. robustus* Prasad, Jaeger, Sahni, Gheerbrant and Khajuria, 1994), and gondwanatherian mammal (*Bharatherium bonapartei* Prasad, Verma, Sahni, Krause, Khosla and Parmar, 2007a) (Krause *et al.*, 1997; Wilson *et al.*, 2007).

An adjacent and correlative intertrappean section of Rangapur also yielded a eutherian mammal *Sahnitherium rangapurensis* Rana and Wilson, 2003 in addition to fish, crocodylian, ostracod, and charophyte taxa (Rana, 1988).

Gokak (Upparhatti): Mammalian teeth referable to gondwanatherian mammal *Bharatherium bonapartei* were described from 3-4 m thick supposed Maastrichtian intertrappean section exposed northwest of Upparhatti village near Gokak town in Belgaum District, Karnataka (Wilson *et al.*, 2007). The intertrappean beds of this area also yielded freshwater molluscs (Kelkar and Gupte, 1943) and turtle remains (de Lapparent de Broin and Prasad, 2020).

Nagpur: From a vertebrate palaeontological point of view, the intertrappean beds of Nagpur, generally known as Takli intertrappean beds are one of the earliest explored beds. This intertrappean section is situated within Nagpur town about 4 km northeast of Nagpur railway station near Takli. A large number of lower vertebrates represented by fish (including otolith based species), amphibians, lizards, and dinosaur remains were reported from this site in the past (Sahni *et al.*, 1982; Gayet *et al.*, 1984; Vianey-Liaud *et al.*, 1987; Rana and Sahni, 1989; Nolf *et al.*, 2008) in addition to ostracods and charophytes (Bhatia and Rana, 1985; Bhatia *et al.*, 1990). The presence of myliobatid *Igdabatis* and dinosaur remains confirm the Late Cretaceous age for this intertrappean section. The most significant finding from this site is the Laurasian frog Pelobatidae gen. et sp. indet. (Sahni *et al.*, 1982).

Mohagaonkalan–Mandla sector: A large number of plant fossils have been documented from the intertrappean beds of Chhindwara (Mohagaonkalan) and Mandla District for long. Most of these intertrappean beds comprise cherts that preserved fossil leaf, flower, fruit, and seed impressions which offer an insight into the plant life during the northward flight of India. The intertrappean beds of Mohagaonkalan were originally considered early Tertiary in age (Sahni, 1934; Prakash, 1960; Bande *et al.*, 1986), but recent palynological studies have documented the presence of Maastrichtian palynofossils and dinosaur eggshells favouring a Late Cretaceous age (Srinivasan, 1996; Kar and Srinivasan, 1997; Kumaran *et al.*, 1997; Thakre *et al.*, 2017). The most interesting discoveries from the Deccan intertrappean beds of Central India include the oldest records (fruits and seeds) of the grape family Vitaceae (*Indovitis chitaleyae* Manchester, Kapgate and Wen, 2013), leaf impressions of the Dipterocarpaceae family (*Dipterocarpus dindoriensis* Khan, *et al.*, 2020), fruit fossils belonging to the family Phyllanthaceae within the euphorbioid clade of Malpighiales (*Phyllanthocarpon singpurensis* Kapgate *et al.*, 2017), fossil coconut (*Cocos binoriensis* Srivastava and Srivastava, 2014), and wood fossils (*Connaroxylon dimorphum* Baas,

Manchester *et al.*, 2017) referable to the family Connaraceae.

Bombay: The intertrappean black shales of Bombay, particularly those of Worli Hill and Malabar Hill, are famous for their articulated frog skeletons and are often referred as 'frog beds' (Chiplonkar, 1940; Verma, 1965). Though these intertrappean beds were regarded as Eocene in age (Chiplonkar, 1940), later study from Amboli quarry has indicated a Late Cretaceous (Maastrichtian) age (Singh and Sahni, 1996). This site has yielded the dorsoventrally flattened skull of *Sankuchemys sethnai* Gaffney, Sahni, *et al.*, 2003, a turtle species belonging to the Indian tribe Kurmademydini.

Kisalपुरi: The intertrappean section of Kisalपुरi exposed 1.5 km southwest of Kisalपुरi village, Dindori District, Madhya Pradesh is the fourth mammal-yielding intertrappean site besides Naskal, Rangapur, and Upparhatti. This 4.5 m thick siltstone, mudstone, clay sequence is one of the richest vertebrate fossil yielding intertrappean horizon that has produced myliobatid *Igdabatis* (Verma *et al.*, 2017), lepisosteid, osteoglossid, siluriform and pycnodontid fish, ?Costata, leptodactyloid-hemisotid, ranoid-myobatrachoid and ?ranoid anurans, Bothremydidae turtles, indeterminate squamates (Rage *et al.*, 2020), crocodylian teeth, turtle, crocodylian (Khosla *et al.*, 2009; Prasad *et al.*, 2015) and dinosaur eggshells, and eutherian (*Deccanolestes narmadensis* Prasad *et al.*, 2010; *Kharmerungulatum vanvaleni* Prasad *et al.*, 2007b) and gondwanatherian (*Bharatherium bonapartei* Prasad *et al.*, 2007a) mammals. The fauna also includes freshwater gastropods and ostracods. This intertrappean site was considered Maastrichtian in age because of the presence of myliobatid *Igdabatis* and dinosaur remains (Khosla *et al.*, 2004).

Kallamedu Formation, Cauvery Basin: The Kallamedu Formation is the youngest Cretaceous formation of the Cauvery Basin and is the only continental deposit of the predominantly shallow marine Cretaceous succession of this basin. The Kallamedu outcrops containing red clays, friable sandstone, and sandy clays are exposed in badlands to the east and northeast of Kallamedu village located about 10 km to the northeast of Ariyalur town, Tamil Nadu. The basal part of the formation indicates marine influence as evident from the presence of planktic foraminifers (Srivastava and Tewari, 1967), while the vertebrate fossils (such as fish, amphibians, turtles, crocodiles, and dinosaurs) yielding the upper part was interpreted to have been deposited in a flood plain environment during the latest Cretaceous (Tewari *et al.*, 1996). The Kallamedu formation long known for its fragmentary dinosaur bones and teeth (Blanford, 1862; Matley, 1929), contains some palaeobiogeographically significant elements like phyllodontid fish *Egertonia*, bothremydid turtle *Kurmademys kallamedensis* Gaffney, Chatterjee and Rudra, 2001, notosuchian crocodile cf. *Simosuchus*, abelisaurid (Prasad *et al.*, 2013), and troodontid dinosaurs (Goswami *et al.*, 2013).

SIGNIFICANT FOSSILS FINDS

Close examination of the Cretaceous vertebrate fauna of India reveals the presence of clades either having restricted

distribution in southern hemisphere continents or northern hemisphere continents as well as biota that evolved during insular India's northern voyage and those dispersed into India from other continents.

Anurans

The Cretaceous anuran fossils of India include forms having restricted distribution in Gondwana such as Leptodactylidae indet. (Fig. 2.4), Hemisotidae indet., Hylidae indet., Ranoidea indet. along with those that originated in Laurasia, for example, Pelobatidae indet., *Costata incertae sedis*, Gobiatinae indet. (Fig. 2.1-2.3) (Sahni *et al.*, 1982; Prasad and Rage, 1991; 1995; 2004).

Lizards

The family Anguidae with which some of the lizard remains from the intertrappean beds of Naskal were identified (Fig. 3.1-3.3) (Prasad and Rage, 1995) originated in Laurasia and was not found in pre-Cenozoic fossil record of southern continents. It's presence in the Late Cretaceous of India points towards possible faunal dispersal from the north in the Late Cretaceous.

Turtles

Kurmademys kallamedensis (Gaffney *et al.*, 2001) from the Kallamedu Formation and *Sankuchemys sethnaei* (Gaffney *et al.*, 2003) from the intertrappean beds of Bombay nest with *Kinkonychelys rogersi* of the Upper Cretaceous Maevarano Formation, Madagascar in the tribe Kurmademydini (*Sankuchemys* (*Kinkonychelys*+*Kurmademys*)) (Gaffney *et al.*, 2006). Based on this close relationship of Indian Late Cretaceous bothremydid taxa to *Kinkonychelys*, Gaffney *et al.* (2006) suggested that a terrestrial connection existed between India and Madagascar in the latest Cretaceous. Earlier, the fossil turtles described from the Lameta Formation and intertrappean beds were generally assigned to Pelomedusoides, a Gondwanan clade. The latest study of turtle cranial (Plate II, Figs 1, 2) and postcranial bones from the intertrappean beds of Upparhatti suggest that the Indian Cretaceous turtles are endemic to India at genus level (de Lapparent de Broin and Prasad, 2020). Recently, *Shweboemys pisdurensis* known from the Lameta Formation of Pisdura (Jain, 1977; 1986) was re-described as a new combination *Jainemys pisdurensis* and was placed within the clade Kurmademydini as a sister taxon to *Sankuchemys sethnaei* (Joyce and Bandyopadhyay, 2020). Since Kurmademydini is restricted to the Late Cretaceous of India and Madagascar, it was concluded that the Late Cretaceous turtle fauna is partially endemic to India (Joyce and Bandyopadhyay, 2020).

Snakes

Two families of snakes, viz., Madtsoiidae and Nigrophidae, are known to occur in the Lameta and intertrappean outcrops of India. The madtsoiids represented

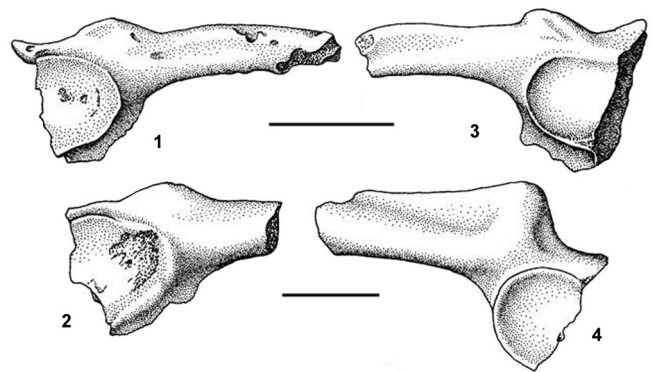


Fig. 2. Anuran ilia from the Upper Cretaceous intertrappean beds of Naskal, Rangareddi District, Telengana. 1-3. Gobiatinae indet., 1. right ilium (VPL/JU/1016) in lateral view, 2. right ilium (VPL/JU/1018) in lateral view, 3. left ilium (VPL/JU/1017) in lateral view, 4. ?Leptodactylidae or Hemisotidae indet., left ilium (VPL/JU/1021) in lateral view. Scale bar equals 2 mm. All images are adapted from Prasad and Rage (2004).

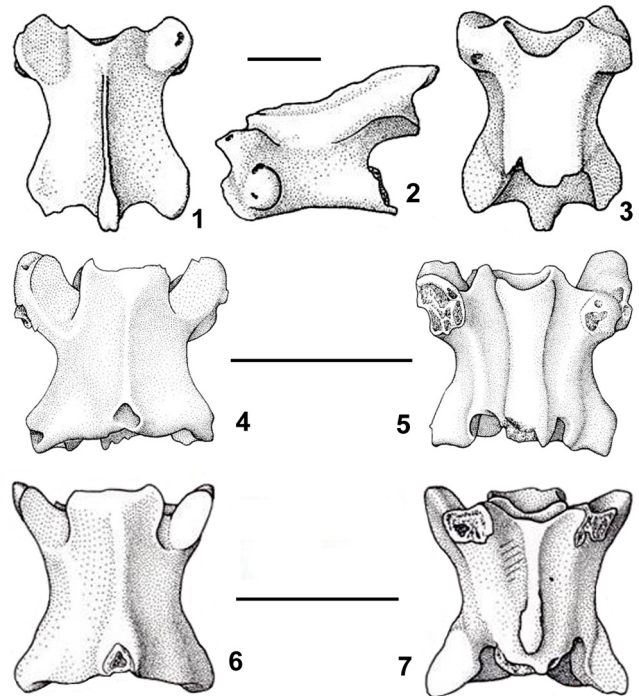
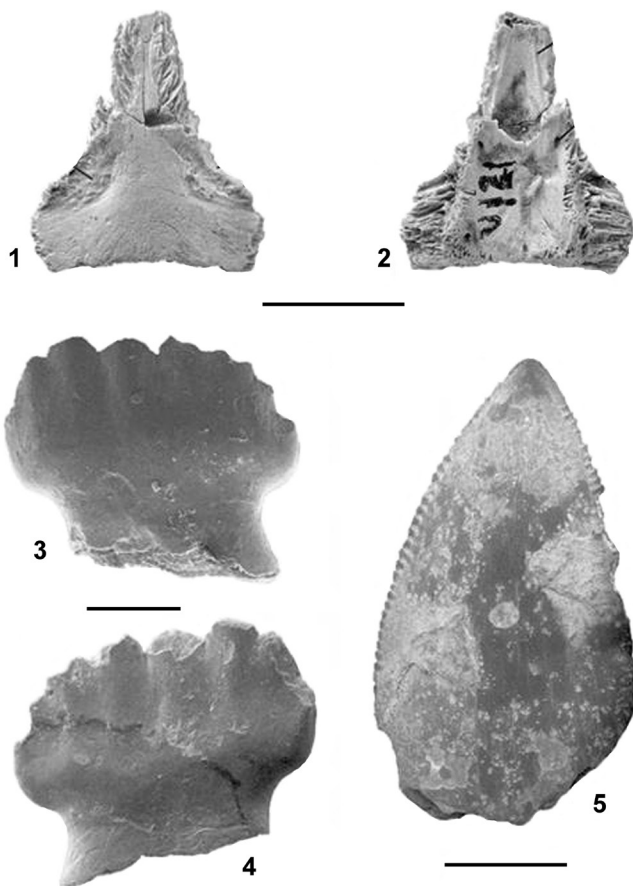


Fig. 3. 1-3. Anguidae gen. et sp. indet. (VPL/JU/1200) from the Upper Cretaceous intertrappean beds of Naskal, Rangareddi District, Telengana, 1. dorsal view, 2. left lateral view, 3. ventral view. 4-5. Madtsoiidae indet., posterior trunk vertebra (VPL/JU/1519) from the Upper Cretaceous intertrappean beds of Kelapur, Yeotmal District, Maharashtra, 4. dorsal view, 5. ventral view. 6-7. *Indophis sahni* Rage and Prasad, 1992, mid trunk vertebra (VPL/JU/500), holotype from the Upper Cretaceous intertrappean beds of Naskal, Rangareddi District, Telengana, 6. dorsal view, 7. ventral view. Scale bar equals 1mm for 1-3 and 2 mm for 4-7. Images 1-3, 4-5, and 6-7 are adapted from Prasad and Rage (1995), Rage *et al.* (2004), and Rage and Prasad (1992), respectively.

by *Sanajeh indicus* Wilson, Mohabey, Peters and Head, 2010, *Madtsoia pisdurensis* (Mohabey, Head and Wilson, 2011) from the Lameta Formation and Madtsoiidae indet. (Fig. 3.4-3.5) from the intertrappean beds (Rage *et al.*, 2004) have a typical Gondwana distribution (South America, Africa, Madagascar, India, and Australia). They were also



EXPLANATION OF PLATE I

Plate I. 1-2. Basisphenoid of *Bothremyidae* gen. et sp. indet. (DUGF/T167) from the intertrappean beds of Upparhatti, Karnataka, 1. ventral view, 2. dorsal view. 3-4. Distal tooth of notosuchid crocodile, cf. *Simosuchus* sp. (DUGF/48) from the Upper Cretaceous Kallamedu Formation, Cauvery Basin, 3. labial view, 4. lingual view. 5. *Abelisauridae* indet. (DUGF/53) from the Upper Cretaceous Kallamedu Formation, Cauvery Basin, labial view. Scale bar equals 1cm for 1-2, 1mm for 3-4, 5 mm for 5. Images 1-2 and 3-5 are adapted from De Lapparent de Broin and Prasad (2020) and Prasad et al. (2013), respectively.

documented in southern Europe (France and Spain) by Rage (1996). *M. pisdurensis* exhibits many morphological similarities with *M. madagascarensis* from the Upper Cretaceous Maevarano Formation of Madagascar (Mohabey et al., 2011). Likewise, Nigerophiidae *Indophis sahnii* (Fig. 3.6-3.7) shares many morphological features with *Kelyophis hechti* reported from Madagascar pointing to their close relationship (LaDuke et al., 2010). The recent discovery of a second species of *Indophis* (*Indophis fanambinana* Pritchard et al., 2014) from the Maevarano Formation further provides strong evidence for a biogeographic link between India and Madagascar in the Late Cretaceous.

Crocodiles

A notosuchid crocodilian tooth mimicking the crown morphology of *Simosuchus clarki* Buckley, Brochu, Krause and Pol, 2000 of Madagascar (Kley et al., 2010) was reported

from the Kallamedu Formation (Plate I, Figs 3, 4) (Prasad et al., 2013). As *Simosuchus* is not known in other Gondwanan or Laurasian landmasses and is restricted to Madagascar and India, it implies a close connection between these two landmasses in the Late Cretaceous. It is also pertinent to mention here that a partial rostrum and dentary of a crocodile designated as *Pabweshi pakistanensis* Wilson et al., 2001 described from the Upper Cretaceous (Maastrichtian) Pab Formation of Pakistan is the only baurusuchid crocodile known outside South America. Since South America was well separated from India by the Late Cretaceous, *Pabweshi* may represent the basal stock that existed in the Indian subcontinent when its contact with South America was still intact during the Early Cretaceous.

Dinosaurs

The Late Cretaceous dinosaur fauna of India is represented by herbivorous titanosaurid sauropods (*Jainosaurus septentrionalis*, *Isisaurus colberti*, Titanosauriformes indet.) and carnivorous abelisaurid theropods (*Indosuchus raptorius*, *Indosaurus matleyi*, *Rajasaurus narmadensis*, *Laevisuchus indicus*, *Rahiolisaurus gujaratensis*) and Maniraptoria (Troodontidae).

The titanosaurid dinosaurs were considered to have achieved global distribution following their origin in pre-break-up Pangaea (Wilson and Sereno, 1998), and their absence in mid-Cretaceous of Euramerica was attributed either to sampling bias (Wilson and Upchurch, 2003) or to regional extinction that was followed by dispersal from the southern continents (Le Loeuff, 1993).

The common occurrence of abelisauroid theropods (Plate I, Fig. 5) in South America, Africa, India, and Madagascar can be explained by a vicariance evolutionary pattern that involves early Cretaceous radiation in Gondwana before its fragmentation and evolution of endemic lineages in the mid-Cretaceous following the break-up of Gondwana (Sereno et al., 2004). Recent phylogenetic analysis of Late Cretaceous abelisaurid taxa such as *Majungasaurus* from Madagascar, *Indosaurus*, *Rajasaurus*, and *Rahiolisaurus* from India, and *Arcovenator* from southern Europe placed them in the *Majungasaurinae* lineage that evolved from a common ancestor independently from those of South America and Africa (Tortosa et al., 2014). This implies that close terrestrial links were present in the Late Cretaceous between India, Madagascar, and Europe facilitating the dispersal of taxa belonging to *Majungasaurinae*.

Troodontid dinosaurs had a wide geographic distribution in Laurasia and until now no troodontid was documented from Gondwana. The discovery of a solitary tooth of troodontid from the Kallamedu Formation extends this primarily Laurasian theropod clade into India (Goswami et al., 2013). This brings us to the question of whether there was a dispersal event from Laurasia involving troodontid dinosaurs in the Late Cretaceous or was there a previously unknown distribution of this group in Gondwana.

Mammals

Gondwanatheres: Hypsodont gondwanathere mammals,

originally reported from the Campanian and Palaeocene rocks of South America (*Gondwanatherium patagonicum* Bonaparte, 1986a; *Sudamerica ameghinoi* Scillato-Yané and Pascual, 1984; *Ferugliotherium windhausenii* Bonaparte, 1986b (Krause *et al.*, 1992; Krause and Bonaparte 1993)), were later documented from the Upper Cretaceous Maevarano Formation of Madagascar (*Lavanify miolaka* Krause *et al.*, 1997) and the intertrappean beds of Naskal (Plate II, Figs 6, 7) (Sudamericidae *incertae sedis* (Das Sarma *et al.*, 1995; Krause *et al.*, 1997; *Bharattherium bonapartei* Prasad *et al.*, 2007b)). Subsequently more gondwanatherian taxa were described from the intertrappean beds of Naskal, Upparhatti and Kisalपुरi (*Bharattherium bonapartei* Prasad *et al.*, 2007a; Wilson *et al.*, 2007), from the Campanian–Maastrichtian deposits of Argentina (*Trapalcotherium matuastensis* Rougier *et al.*, 2009), from the Palaeogene deposits of Argentina (*Greniodon sylvaticus* Goin *et al.*, 2012) and Antarctica (Sudamericidae gen. et sp. indet., cf. *Sudamerica ameghinoi*; Goin *et al.*, 2006), the Upper Cretaceous (late Turonian–latest Campanian) Galula Formation (Krause *et al.*, 2003; *Galulatherium jenkinsi* O'Connor *et al.*, 2019) of southwestern Tanzania and the Maevarano Formation of Madagascar (*Vintana sertichi* Krause, 2014; *Adalatherium hui* Krause *et al.*, 2020) and from the Upper Cretaceous (Campanian–Maastrichtian) Dorotea and Chorrillo formations of Chile and Argentina, respectively (*Magallanodon baikashkenke* Goin *et al.*, 2020; Chimento *et al.*, 2021). These fossil records indicate a pan-Gondwanan distribution for this enigmatic group of mammals. Recent phylogenetic analysis of gondwanatherian mammals recognized a node consisting of *Vintana*, *Lavanify*, and *Bharattherium* excluding all South American and African taxa (Krause, 2014). This provides important evidence for the isolation of the Indo–Madagascar lineage from other Gondwanan continents in the Late Cretaceous which is consistent with a vicariance biogeographic scenario.

Further, based on the discovery of grass phytoliths in the coprolites of titanosaurid dinosaurs from the Lameta Formation of Pisdura; it was proposed that grasses belonging to extant Poaceae were present in the Indian subcontinent and other Gondwanan landmasses in the Late Cretaceous because of vicariant evolution or dispersals (Prasad *et al.*, 2005). The co-occurrence of the high-crowned gondwanatherian mammals and grass phytoliths in the Upper Cretaceous deposits of India led these authors to suggest that gondwanatheres adapted for eating hard food materials like grasses and the two groups evolved together.

Haramiyids: Traditionally the haramiyid mammals have been documented from the Upper Triassic–Middle Jurassic deposits of North America, Europe, and Asia (Kielan-Jaworowska *et al.*, 2004). Fossil records of these mammals from the Upper Jurassic and Cretaceous deposits of the Gondwanan continents are few and are restricted to the Upper Jurassic Tendaguru beds of Tanzania (Heinrich, 1999; 2001), Upper Jurassic–Lower Cretaceous Ksar Metlili Formation of Morocco (Sigogneau-Russell, 1991; Hahn and Hahn, 2003; Huttenlocker *et al.*, 2018) and the Upper Cretaceous infratrappean beds of Bacharam, Rangareddi District, Telangana (Anantharaman *et al.*, 2006). *Avashishta bacharamensis*, the Late Cretaceous haramiyid from India with close morphological similarities to the teeth of

Allostaffia aenigmatica (Heinrich, 2001) from the Upper Jurassic Tendaguru beds of Tanzania was interpreted as a late survivor of the group from a Gondwanan stock on physically isolated Indian subcontinent (Anantharaman *et al.*, 2006).

Eutherians: Confirmed eutherian mammals from Gondwana are known only from the Upper Cretaceous intertrappean beds of Naskal, Rangapur and Kisalपुरi (Prasad and Sahni, 1988; Prasad *et al.*, 1994; Rana and Wilson, 2003; Khosla *et al.*, 2004; Prasad *et al.*, 2007b, 2010, Wilson *et al.*, 2022). Phylogenetic analysis of the majority of these mammalian taxa (*Deccanolestes hislopi* Prasad and Sahni, 1988 (Plate II, Figs 1, 2, 3), *D. robustus* Prasad, Jaeger, Sahni, Gheerbrant and Khajuria, 1994 (Plate II, Fig. 4), *D. narmadensis* Prasad, Verma, Gheerbrant, Goswami, Khosla, Parmar and Sahni, 2010, *Sahnitherium rangapurensis* Rana and Wilson, 2003) placed them in the family Adapisoriculidae as sister taxa to the Palaeogene adapisoriculid *Afrodon* from northwest Africa and Europe. The recent report of an adapisoriculid *Bharatlestes kalami* from the Lower Eocene Cambay Shale (Kapur *et al.*, 2017a; 2017b) attests to the survival of this mammalian group beyond the Cretaceous–Palaeogene (K/Pg) boundary. Since the Indian adapisoriculids are relatively primitive and older as compared to African and European forms, it is inferred that India was the center of origin for adapisoriculids, and dispersal to Africa and Europe took place close to the K/Pg boundary (Prasad *et al.*, 2010; Smith *et al.*, 2010; Goswami *et al.*, 2011). More recently, two more eutherian species, *Indoclemensia naskalensis* and *I. magnus* were reported from the intertrappean beds of Naskal (Wilson, *et al.*, 2022).

An archaic ungulate-like mammal (*Kharmerungulatum vanvaleni* Prasad, Verma, Sahni, Parmar and Khosla, 2007b) with tooth morphology very similar to those of *Protungulatum*, *Oxyprimus*, *Baiococonodon*, and *Mimatuta*, archaic ungulates from the Late Cretaceous–Early Palaeocene of North America, was recovered from the Upper Cretaceous intertrappean beds of Kisalपुरi, Central India (Plate II, Fig. 5) (Prasad *et al.*, 2007b). Though cladistic analysis of eutherian taxa from India did not show *Kharmerungulatum* as a placental mammal (Goswami *et al.*, 2011), in a recent phylogenetic treatment of an ungulate-like mammal *Pahelia mysteriosa* from the Lower Eocene Cambay Shale (Zack *et al.*, 2019) *Kharmerungulatum* was recovered as close to *Oxyprimus* and *Mioclaenus* of North America. This points to a possible Late Cretaceous dispersal event involving Euramerica. However, as this evidence is based on a single, worn lower molar, a final verdict on this possible biogeographic event must await better preserved additional fossil material.

RELEVANCE OF CRETACEOUS FOSSILS IN THE CONTEXT OF INSULAR INDIA

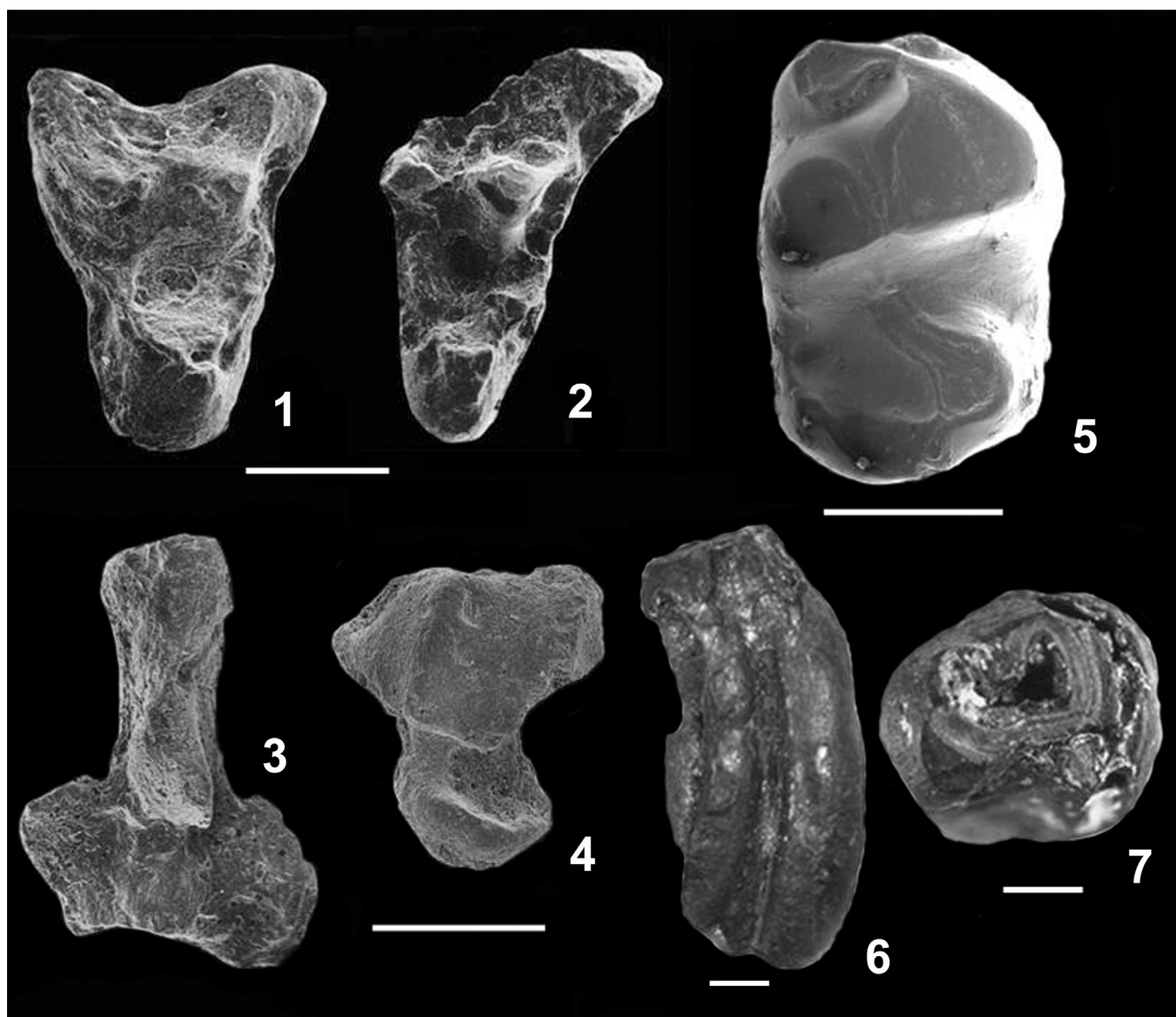
Critical evaluation of fossil biota from the Cretaceous deposits of India presents mixed palaeobiogeographic patterns. In the past, the presence of leptodactylid, hemisotid, hylid, and ranoid frogs, madtsoiid and nigerophiid snakes,

baurusuchid crocodiles, pelomedusoid turtles, abelisaurid dinosaurs, and gondwanathere mammals was explained by dispersals across a terrestrial connection between South America and Indo–Madagascar via Antarctica and Kerguelen Plateau / Gunnerus Ridge (Krause *et al.*, 1997; Hay *et al.*, 1999; Prasad and Sahni, 1999; Case, 2002). However, this palaeobiogeographic model was discarded as geophysical data from the southern Indian Ocean revealed that the Kerguelen Plateau / Gunnerus Ridge was submerged beneath ocean water in the Late Cretaceous (Ali and Aitchison, 2009; 2011). Moreover, the taxonomic position of most of the Gondwanan taxa is not known below the family or even the ordinal level. For example, leptodactylid, hemisotid, hylid, and ranoid frogs might represent the taxa that survived on the Indian subcontinent from a basal stock that had pan-Gondwana distribution when the southern continents were connected. Likewise, phylogenetic analysis of abelisaurid dinosaurs indicates that the morphological similarities between the Indo–Madagascar Late Cretaceous taxa and those of South America are of plesiomorphic characters retained from pan-Gondwanan ancestral clades (Tortosa *et al.*, 2014). Following the break-up of Indo-Madagascar block from other Gondwanan continents in the mid-Cretaceous, they underwent vicariant evolution leading to the development of a lineage in India and Madagascar that is distinctly different from that of South America. This vicariant biogeographic pattern is consistent with Smith *et al.* (1994) palaeogeographic reconstruction of a terrestrial corridor between South America and the Indian subcontinent through Antarctica until the Early Cretaceous (~130 Ma ago).

The same evolutionary pattern can be inferred for madtsoiid and nigerophiid snakes, bothremydid turtles, and gondwanathere mammals. Phylogenetic analyses resolved *Indophis sahnii* (Nigerophiidae) and *Sankuchemys sethnai–Kurmamedmys kallamedensis* (Kurmamedyidini) of India as sister taxa of *Indophis fanambinana* (Nigerophiidae) and *Kinkonychelys rogersi* (Kurmamedyidini) of Madagascar, respectively (Gaffney *et al.*, 2006; Pritchard *et al.*, 2014). Gondwanathere mammals from India (*Bharattherium bonapartei*) and Madagascar (*Lavanify miolaka* and *Vintana sertichi*) share derived characters to the exclusion of the taxa from South America, Antarctica, and Africa (Krause, 2014). All these turtle, snake, dinosaur, and mammal taxa together with simosuchid crocodiles (*Simosuchus*) and phyllolepid fish (*Egertonia*) favour a close biogeographic connection between India and Madagascar through some intervening microcontinental slivers such as Lakshmi Ridge, the Seychelles Plateau, Amirante Ridge, Providence Bank and other concealed microcontinents (Parmar and Prasad, 2020). Assuming that these phylogenetic relationships are correctly interpreted, their distribution is more consistent with a classic vicariance biogeographic scenario.

The Cretaceous isolation of India also made possible the evolution of endemic lineages of different animal and plant groups. Recent taxonomic studies of cranial and postcranial bones of pleurodire turtles from the Cretaceous rocks of India demonstrated that many of these taxa were endemic to India (de Lapparent de Broin and Prasad, 2020; Joyce and Bandyopadhyay, 2020). The Cretaceous eutherian mammals *Deccanolestes* and *Sahnitherium* placed in the family Adapisoriculidae (Prasad *et al.*, 2010; Smith *et al.*, 2010; Goswami *et al.*, 2011) are the only known eutherian mammals

from Gondwana and represent the oldest occurrence of Adapisoriculidae. As closely related *Afrodon* and *Bustylus* are known from the younger Early Palaeocene and Late Palaeocene deposits of Belgium (Smith *et al.*, 2010) and NW Africa (Gheerbrant, 1988), respectively, it was concluded that adapisoriculids had originated on insular India and later dispersed out of India (Prasad *et al.*, 2010; Smith *et al.*, 2010; Goswami *et al.*, 2011). The recent report of an adapisoriculid (*Bharatlestes kalami*) that is more derived than *Deccanolestes* from the Lower Eocene Cambay Shale (Kapur *et al.*, 2017a; 2017b) confirms the survival of Cretaceous/Palaeogene boundary mass extinction event by this group of mammals. Remarkable endemism was also noticed in the freshwater ostracod fauna of the Deccan intertrappean beds. The highly diverse intertrappean ostracod fauna with an overwhelmingly high percentage (98%) of endemic species favor India as a center of origin for these species with some of them dispersing out of India (Whatley and Bajpai, 2000; Whatley, 2012). New finds of plant fossils from the Deccan intertrappean beds further add to the growing number of taxa that are identified to have had an Indian origin. The documentation of fossil fruits and seeds of vine family Vitaceae from the Upper Cretaceous intertrappean beds of Maharashtra and Central India represents the first record of pre-Palaeogene fossils of this family (Manchester *et al.*, 2013). Named *Indovitis chitaleyae*, these fossils are at least 8–10 million years older than their fossil records from the Palaeogene rocks of North America and Europe and contradict the long-held view that the grape family originated in Laurasia and arrived in India following India/Asia collision. Based on its oldest occurrence in physically isolated India, it was suggested that it evolved in India or Madagascar, and/or Africa and later dispersed out of India after its collision with Asia (Manchester *et al.*, 2013). Another fossilized fruit belonging to the family Phyllanthaceae within the euphorbioid clade of Malpighiales (*Phyllanthocarpon singpurensis* Kapgate *et al.*, 2017) was described from the Upper Cretaceous intertrappean beds of Singpur in Chhindwara District, Madhya Pradesh. Before this find, fruits of euphorbiaceous clade were reported from the Eocene deposits of North America and Europe (see Kapgate *et al.*, 2017). *Phyllanthocarpon* from the intertrappean beds is therefore another example of a plant group that originated in insular India and dispersed to northern landmasses in a post-India/Asia collision dispersal event. Similarly, plants belonging to the family Dipterocarpaceae were traditionally considered to have originated in Southeast Asia because of the high diversity of modern dipterocarp species in Southeast Asia and the presence of the oldest and confirmed megafossils of dipterocarps in the Eocene of China and Neogene of India (Bande and Prakash, 1986; Maberley, 1997). However, recent works brought to our knowledge the presence of pollen of these plants in Lower Eocene Cambay Shale (Rust *et al.*, 2010; Dutta *et al.*, 2011) and Upper Cretaceous intertrappean beds of Yeotmal, Maharashtra (Prasad *et al.*, 2018). Their presence in the Late Cretaceous is further confirmed by the recent report of leaf impressions of *Dipterocarpus dindoriensis* from the intertrappean beds of Mandla (Khan *et al.*, 2020). Based on this discovery, Khan *et al.* (2020) suggested that Dipterocarpaceae plants either originated in India during its isolated phase or somewhere else in Gondwana, and reached Asia across India, supporting out of India dispersal hypothesis. A fossil coconut, *Cocos*



EXPLANATION OF PLATE II

1-3. *Deccanolestes hislopi* Prasad and Sahni, 1988 from the Upper Cretaceous intertrappean beds of Naskal. 1. right upper first molar (M^1) (VPL/JU/NKIM/10) in occlusal view, 2. right upper third molar (M^3) (VPL/JU/NKIM/11) in occlusal view, 3. left calcaneum (VPL/JU/NKIM/50) in dorsal view. 4. *Deccanolestes robustus* Prasad, Jaeger, Sahni, Gheerbrant and Khajuria, 1994, right astragalus (VPL/JU/NKIM/51) from the Upper Cretaceous intertrappean beds of Naskal in dorsal view. 5. *Kharmarungulatum vanvaleni* Prasad, Verma, Sahni, Parmar and Khosla, 2007b from the Upper Cretaceous intertrappean beds of Kisalpuri, Dindori District, Madhya Pradesh, right upper first or second molar (M^1 or M^2) (VPL/JU/IM/31) in occlusal view. 6-7. Cheek tooth (VPL/JU/NKIM/25) of *Bharattherium bonapartei* Prasad, Verma, Sahni, Krause, Khosla and Parmar, 2007a from the Upper Cretaceous intertrappean beds of Naskal, Rangareddi District, Madhya Pradesh. 6. lateral view, 7. occlusal view. Scale bar equals for 0.5 mm for 1-2, 1mm for 3-4, 0.9 mm for 5, 0.94 for 6, and 0.97 for 7. 1-2, 3-4, 5, and 6-7 are adapted from Prasad et al. (1994), Prasad and Godinot (1994), Prasad et al. (2007b) and Prasad et al. (2007a), respectively.

binoriensis Srivastava and Srivastava, 2014 was described from the Upper Cretaceous intertrappean beds of Central India. Though several fossil specimens of *Cocos* were reported from the Palaeogene and Neogene deposits of South America, Australia, New Zealand, and India, the fossil specimen from the middle-late Palaeocene of Colombia was considered as the oldest record until now (Gomez-Navaro et al., 2009). Together with various other previous reports from the Deccan intertrappean beds, such as *Palmocarpon cocoides*, *Cocos intertrappeanensis*, *C. nucifera*, *C.*

pantii, and *Palmoxylon (Cocos) sundaram*, (see Srivastava and Srivastava, 2014 for references), *Cocos binoriensis* supports India as the center of origin for *Cocos*, with a later dispersal into Southeast Asia. Wood fossils (*Connaroxylon dimorphum*) referable to the family Connaraceae from the intertrappean beds of Mandla present another example of the oldest record of a plant family that had its origin in India and later dispersed to Asia (Baas et al., 2017).

In addition to these biogeographic scenarios, there are some fossil evidence in support of India's connection

with Eurasia in the Late Cretaceous when it is said to be fully surrounded by marine water. As early as 1982, the presence of Pelobatidae, a Laurasian family of frogs in the Upper Cretaceous Deccan intertrappean beds of Nagpur was cited as evidence for a biotic link between India and Eurasia (Sahni *et al.*, 1982). Additional vertebrate fossil evidence for a northern connection with India came from the intertrappean Gobiatinae frogs and Anguillidae lizards (Prasad and Rage, 1991; 1995; 2004). The recent documentation of a solitary troodontid dinosaur tooth from the Upper Cretaceous Kallamedu Formation if confirmed with additional material would form another evidence for the dispersal of Laurasian taxa into India (Goswami *et al.*, 2013). Archaic ungulate-like mammal, *Kharmerungulatum vanvaleni* from the Upper Cretaceous intertrappean beds of Kisalpur with morphological similarities to *Protungulatum*, *Oxyprimus*, *Baioconodon* and *Mimatuta* from the Late Cretaceous-Palaeocene of North America also support biotic dispersal between India and Laurasia (Prasad *et al.*, 2007b). This is also the case with the report of a coryphoid palm, *Sabalites dindorensis* of Laurasian origin from the Upper Cretaceous intertrappean beds of Central India (Srivastava *et al.*, 2014). Further, many charophyte taxa reported from the intertrappean beds of India exhibit close biogeographic affinities to those of Asia and Europe (Bhatia *et al.*, 1990; Srinivasan *et al.*, 1994; Khosla, 2014). These anomalous occurrences of Laurasiatic elements in insular India have been explained in terms of dispersals across island-arc systems such as Kohistan-Dras-Oman (Prasad and Sahni, 1999; 2009; Parmar and Prasad, 2020).

CONCLUDING REMARKS

The present review is an updated version of the evolution of biota on a northward drifting and physically isolated Indian plate and its biogeographic connections during the Cretaceous Period. It shows how focused and integrated research can significantly improve our understanding of a research problem and address many ancillary questions. Intensified research on Deccan Volcanic Province began

with the suggestion that Deccan volcanism was one of the possible causes of the mass extinction at the Cretaceous-Palaeogene boundary. As a result, extensive and intensive prospecting for fossil-bearing intertrappean horizons within the DVP highlighted many richly fossiliferous sections that significantly improved our knowledge of the biotic diversity, age and biogeographic relationships. From as low as 25-30 fossil taxa known before 1980s, the diversity has increased many folds and the composition changed from mostly plant-dominated taxa in the past to a balanced biota comprising invertebrates, vertebrates, and plants. Our current understanding of the Cretaceous fossil record of India clearly shows that the biota is represented by a mixed assemblage consisting of relicts of Gondwana taxa that radiated in insular India and maintained close biogeographic links with the fauna of Madagascar, those having originated in India and later dispersed to other landmasses, and some which have dispersed into India from Eurasia. The recent findings have clearly indicated that the DVP holds many, yet to be revealed surprises on evolutionary radiations. Future research should focus on finding more fossil-rich sites, constraining them chronologically by integrating fossil, palaeomagnetic and radiometric data, and integrated study of the ecosystem as a whole instead of focusing on a single fossil group. The Indian subcontinent also remained physically isolated during the Palaeocene and early part of the Eocene. The fossil record is better documented for the Late Cretaceous and Early Eocene. However, no continental Palaeocene sites with rich fossils have been identified so far. Any future research directed toward finding Palaeocene fossils is expected to fill the existing gaps in the fossil record.

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