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Review Article

An Overview of Recent Advances in the Mesozoic–Palaeogene Vertebrate Paleontology in the Context of India's Northward Drift and Collision with Asia

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This review article summarizes the recent work done in India on fossil vertebrates from the Mesozoic-early Paleogene interval, with focus on the past five years. Advances made during this period highlight the importance of India's vertebrate fossil record in our understanding of the origin and evolutionary history of several vertebrate groups and the dynamics of intercontinental faunal dispersal and vicariance, especially in the context of India's former position in the Gondwanaland and its subsequent separation from the different Gondwana landmasses as it moved northward to finally collide with Asia in the early Paleogene. These studies have led to a better understanding of the mode of evolution of tetrapods on the drifting Indian plate and provide independent constraints to test the traditional models favouring India's physical isolation from all other landmasses, especially during the late Cretaceous phase of its northward drift. Recent data points to faunal interchanges between India, Africa and Europe at or near the K-Pg boundary and also suggests that the Indian landmass was the centre of origin/early evolution for several orders of modern mammals, including cetaceans (whales), perissodactyls (horses, tapirs) and primates.

Keywords: Cretaceous; Palaeogene; Mammals; Evolution; Palaeobiogeography

Introduction

The Indian subcontinent, which was part of the Gondwanaland in the geological past, had a long history of break-up, isolation and rapid northward journey before its collision with the Asian mainland. The historical biogeography of India is, thus, can be divided into four distinct phases, viz., pre-drift phase, early drift phase, late drift phase and pre-collision and collision phase. In a classic paper, Krause and Maas (1990) hypothesized that primates, artiodactyls, perissodactyls and hyaeonodontids evolved on a *Noah's Ark* like Indian plate during its northward flight, and subsequently dispersed out of India into Asia. This laid the foundation for the later 'Out-of-India' dispersal hypothesis of Bossuyt and Milinkovitch (2001) which was based on molecular phylogeny of modern ranid frogs. In this context, many questions arise regarding the evolution of biota on a drifting landmass – Was there an endemic evolution of biota in response to a long period of isolation? Were there biotic interchanges between India and other landmasses during the former's physical isolation? Is there any fossil evidence for 'Out-of-India' dispersal hypothesis? Therefore, to understand the response of continental vertebrate fauna to India's northward movement from a pre-drift southern high latitude position to its current post-collision position, one must examine the Mesozoic – Palaeogene fossiliferous deposits of the Indian subcontinent. In this short review, the work done in the last five years in different sedimentary basins (Gondwana basins, Cauvery basin, Deccan volcanic province, Tertiary basins of western India and NW Himalaya) representing various phases of India's northward journey is discussed. The main objective of this review is to summarize the recent work done in India in the field of vertebrate palaeontology, especially during the past five years (2011-2015).

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Recent Finds

Pre-drift Phase

During the pre-drift phase India was positioned in the southern high latitudes in the neigbourhood of Africa, Antarctica and Australia and the vertebrate fossil record for this phase has been fairly well documented from the Lower Triassic Panchet Formation, the Upper Triassic Maleri and Tiki formations and the Lower Jurassic Kota Formation of peninsular India through the efforts of researchers from the Geological Studies Unit, Indian Statistical Institute and the Geological Survey of India. Among the lower Triassic rocks of India, the Panchet Formation of Damodar valley is long known for its dicynodont fauna. The latest report of three dicynodot skulls, two belonging to *Lystrosaurus* cf. *curvatus* and the third one representing *L. declivis*, indicated that the *Lystrosaurus* fauna of India is correlatable with that of the upper part of Balfour Formation and the overlying Katberg Formation (Early Triassic) of the Barroo Basin, South Africa in its diversity and age (Gupta and Das, 2011). More recently, a graveyard of rhynchosaur, an archosauromorph reptile, interpreted as representing a mass mortality event during sudden flooding was discovered in the Upper Triassic (Early Carnian) Tiki Formation of South Rewa Gondwana basin (Mukherjee and Ray, 2012). The rhynchosaur bones from this site were later identified as belonging to a new species *Hyperodapedon tikiensis*, possibly the most advanced species among rhynchosaurs that represents a postural evolution intermediate between sprawling and erect postures (Mukherjee and Ray, 2014). Contrary to the long held view that archosauromorphs were slow growing, bone histology of *H. tikiensis* revealed these animals were growing fast during juvenile and sub-adult stages (Mukherjee, 2015). The Tiki Formation has also yielded lower jaws of a new large traversodontid cynodont *Ruberodon roychowdhuri* Ray, 2015. Phylogenetic analysis of *R. roychowdhuri* nested it as a sister taxon of *Exaeretodon statisticae* within the clade containing *Gomphodontosuchus*, *Menadon*, *Scalenodontoides*, *Protuberum*, *Ruberodon* and *Exaeretodon* (Ray, 2015). The new taxon allows the correlation of the Tiki Formation with the lower part of the Upper Triassic Maleri Formation, the Isalo II Beds of Madagascar and the upper part of Santa Maria Formation. Novas *et al*. (2011) described a new dinosaur fauna represented by two plateosaurian taxa (*Nambalia roychowdhuri*, *Jaklapallisaurus asymmetrica*), a guaibasaurid and two basal dinosauriformes from the Upper Triassic Maleri Formation (Norian - earliest Rhaetian). From the Lower Dharmaram Formation (Norian-Rhaetian age), Novas *et al*. (2011) have documented basal sauropodomorph and neotheropod remains. This has substantially improved the diversity of Late Triassic dinosaur fauna of India. Further, the study of Novas *et al*. (2011) has demonstrated that the rhynchosaur dominated Lower Maleri Formation is poor in dinosaurs as compared to their high diversity in coeval beds from South America. On the other hand, the archosaur dominated Upper Maleri and Lower Dharmaram formations yielded taxonomically diverse basal sauropodomorphs as was the case with contemporaneous beds from South America and Europe. The latter radiation post-dating Ischigualastian extinction event indicates that the early radiation of dinosaurs was not synchronous across the world. As expected, the Triassic continental vertebrate fauna of India demonstrates close biogeographic affinities with both Gondwanan and Laurasian continents because of the existence of a single supercontinent Pangaea at that time.

The split between Africa and India - Madagascar block took place during the Jurassic Period (~150-160 Ma ago), (see Prasad and Sahni, 1999; Chatterjee *et al*., 2013). The Kota Formation of Pranhita-Godavari valley is one of the few Early Jurassic vertebrate yielding horizons in the world and has been a source of many vertebrate groups including fishes, amphibians (personal observations of the first author), crocodiles, turtles, rhynchocephalians, lizards, dinosaurs, and mammals (see Prasad and Manhas, 2007 for references). Dinosaurs include two nearly complete skeletons (Jain *et al*., 1979; Yadagiri *et al*., 1979; Bandyopadhyay *et al*., 2010). A more detailed description of the skeletal elements of the briefly described sauropod dinosaur *Barapasaurus tagorei* (Jain *et al*., 1979) and some other specimens that have not been studied earlier was provided by Bandyopadhyay *et al*. (2010). Phylogenetic analysis of the various skeletal characters led Bandhyopadhyay *et al*. (2010) to conclude that *Barapasaurus* is more derived than *Kotasaurus*, the second dinosaur taxon of the Kota Formation, but it is more basal to *Vulcanodon*. The upper part of the Dharmaram

Formation of the Pranhita-Godavari valley has also yielded Early Jurassic vertebrates but these are mainly restricted to skeletal remains of two taxa of basal sauropodmorphs (Kutty *et al*., 2007). Outside the Gondwana sedimentary basins of India, footprints of theropod dinosaurs (*Eubrontes* cf. *giganteus*, *Grallator tenuis*) have been documented from the marine Lower Jurassic Thaiat Member of the Lathi Formation, Jaisalmer basin, western India (Pienkowski *et al*., 2015). The mammalian fauna from the Kota Formation assumes great significance as it is expected to reveal the diversity and evolution of early mammals in the former Gondwanaland at a time when the continents began to breakup. Until now, the early mammal groups represented by symmetrodonts, triconodonts, docodonts and multituberculates have been documented from Kota Formation (Parmar *et al*., 2013 for references). In fact, the multituberculate mammal *Indobaatar zofiae* from the Kota Formation is possibly the oldest member of this predominantly Laurasian group (Parmar *et al*., 2013). More recently, Parmar *et al.* (2015) indicated that the mammalian fauna of the Kota Formation is highly diverse consisting of the Gondwanan australosphenidans, haramiyidans, and possible dryolestids, besides the already known symmetrodonts, triconodonts, docodonts and multituberculates. In the former Gondwanaland, besides India, Jurassic mammals are known from South America and Africa. However, in the latter two landmasses, the mammalian diversity is extremely low, with only australosphenidans and dryolestids recorded from South America, and haramiyidans and therians known from Africa. In comparison, the diversity of Indian Jurassic mammals is very high, as diverse as that of Laurasia. This implies very close biogeographic connections between India and Laurasia and biogeographic partitioning of Gondwanan continents during the Jurassic.

Early Drift Phase

During the early drift phase, the Indo-Madagascar block was separated from the Australia-Antarctica block at about 120-130 Ma ago (see Prasad and Sahni, 1999; Chatterjee *et al*., 2013) which was followed by the inundation of southeastern coast of India and deposition of marine Cretaceous sediments in the Cauvery basin, South India (Veevers *et al*. 1991). The vertebrate record for the early drift phase of India is poorly documented. The sedimentary rock record for the Early Cretaceous period is represented by the Dalmiapuram and Karai formations of Cauvery basin, the Gangapur Formation of Pranhita-Godavari valley, informally designated east coast Gondwana rocks, and the Rajmahal intertrappean beds. So far, no animal fossils have been reported from the Rajmahal intertrappean beds. Only isolated fish scale impressions are known from the East Coast Gondwana deposits (Bakshi, 1973). The Cretaceous Gangapur Formation has yielded scarce vertebrate fossils consisting of actinopterygian fish teeth (Prasad *et al*., 2004). In a recent study, Underwood *et al*. (2011) described a fairly large number of shark teeth (*Protosqualus* sp., *Gladoserratus magnus*, ?*Notidanodon* sp., *Cretalamna appendiculata*, *Dwardius sudindicus*, ?*Eostriatolamia* sp., *Squalicorax* aff. *baharijensis* and *Cretodus longiplicatus*) and a few ichthyosaur teeth representing *Platypterygius indicus*? from The Albian – Cenomanian Karai Formation. Most of these shark taxa were endemic to India at species level and many of them had an antitropical distribution consistent with the high latitude position of India. Subsequently, durophagous shark teeth belonging to the cosmopolitan *Ptychodus decurrens* were also documented from the Karai Formation (Verma *et al*., 2012).

Late Drift Phase

Two major plate tectonic events occurred during the late drift phase: 1) break-up of India-Seychelles block from Madagascar around 88-90 Ma ago and 2) eruption of Deccan Traps and separation of India from the Seychelles at about 65 Ma ago. This was also the phase during which the Indian landmass drifted very rapidly at a rate of 15-20 cm/year (Powell, 1979) until its docking with the southern margin of Asia around 50-55 Ma ago (Patriat and Achache, 1984). Therefore, the vertebrate fauna from the late drift and pre-collision phases is very important for understanding the evolution of life on a landmass migrating rapidly towards the north as a Noah's Ark and the effects of large scale volcanism on life. The sedimentary sequences representing the late drift phase are the Upper Cretaceous (Maastrichtian) Lameta Formation and the Deccan intertrappean beds of Deccan Volcanic Province, and the Upper Cretaceous (Late Maastrichtian) Kallamedu Formation of Cauvery basin. The Lameta Formation and the Deccan intertrappean beds have been extensively studied in recent years because of the supposed linkage between Deccan volcanism and the Cretaceous-Palaeogene (K-Pg) boundary mass extinctions (McLean, 1985). As a consequence, the Late Cretaceous biodiversity record of India has improved tremendously in the last three decades (see Prasad and Sahni, 2014 for citations). Currently, the vertebrate fauna from the Lameta Formation and the intertrappean beds is known by 53 species of fishes, 5 species of amphibians, 8 species of lizards, 5 species of turtles, 3 species of crocodiles, 6 species of snakes, 9 species of dinosaurs and 7 species of mammals (Prasad, 2012). The latest report of a partial skeleton of 3.5 m predatory snake named as *Sanajeh indicus* (Family Madtsoidae) from the Lameta Formation exposed near Dholi Dungri village in Gujarat and occurring coiled around a dinosaur egg and adjacent to a hatchling skeleton has suggested that this snake frequented sauropod nesting sites and preyed upon hatchling sauropods (Wilson *et al*., 2010). In a subsequent publication, Mohabey *et al*. (2011) described a new species of a madtsoid snake *Madtsoia pisdurensis* from the Lameta Formation of Pisdura, Maharashtra with close relationship to *M. madagascarensis* from the Late Cretaceous of Madagascar and to *M. bai* and *M. composi* from the Palaeocene of South America. These authors suggested that as India, Madagascar and South America were well separated from each other by 100-90 Ma, the wide distribution of similar taxa in these landmasses indicates their origin and dispersal prior to the separation of these landmasses or that there were some yet to be identified land connections between these southern terranes. Srivastava and Mankar (2015) documented the presence of a single nest of *Megaloolithus* (sauropod dinosaur) in the Lameta Formation from a geographic site located at the boundary of Amaravati District in Maharashtra and Betul District in Madhya Pradesh, quite far away from the traditionally known nesting sites of Jabalpur, Bagh, Balasinor, and Dongargaon. In a major taxonomic reassessment of the purported large lizard nest found in association with sauropod nests in the Lameta Ghat section of the Lameta Formation at Jabalpur, Srivastava *et al*. (2015) reassigned it to crocodiles. This is the first record of a crocodile nest from the Late Cretaceous of India. Fernández and Khosla (2015) revisited the parataxonomic classification of the Late Cretaceous dinosaur eggshells of the Megaloolithidae family from the Lameta Formation of India and the Upper Cretaceous Allen Formation, Argentina and synonymized some of the taxa with the pre-existing ones and also erected a new genus *Fusioolithus* for *M. baghensis* and synonymized *M. pseudomamillare*, *M. balasinorensis*, *Patagoolithus salitralensis* with *Fusioolithus baghensis*. Tipo 1c eggshells of Argentina were referred to a new species of *Fusioolithus, F. berthei*. Since five of the dinosaur oospecies (*M. jabalpurensis*, *M. cylindricus*, *M. megadermus*, *F. baghensis* and *F. berthei*) are common to India, South America, Africa and France, Fernández and Khosla (2015) inferred a close phylogenetic relationship between the dinosaur oospecies of these continents and the existence of a terrestrial connection between India and Europe and between the Gondwanan continents. A detailed analysis of Type A sauropod coprolites from the Lameta Formation of Pisdura, Maharashtra revealed the presence of freshwater ostracods, diatoms, charophytes, sponge spicules, probable chrysophytes, gymnosperm tissues, a spore, cuticle and leaf laminae (Khosla *et al*., 2015). The presence of these plant tissues and microfossil remains in phosphatic coprolites indicates that the producer animals were intentional or passive omnivores.

The latest discoveries from the intertrappean beds have thrown some new light on the origin and evolution of primitive eutherian mammals on insular India. Earlier, based on ankle bone functional morphology, *Deccanolestes*, the well known Late Cretaceous eutherian mammal from India, was inferred as an euarchontan (Prasad and Godinot, 1994; Smith *et al*., 2010), the ancestral stock from which primates had originated. However, Prasad *et al*. (2010) supported by new dental material from the intertrappean beds showed that *Deccanolestes* is phylogenetically close to *Afrodon* (Family Adapisoriculidae) known from the Palaeocene rocks of Africa (Gheerbrant and Russell, 1989) and Europe (Russell, 1964). Because of the older age and slightly primitive state of the Indian taxon, they suggested that *Deccanolestes* originated in India and subsequently dispersed to Africa and Europe close to the K-Pg boundary. In a concurrent publication, based on the study of new postcranial bones (humerus and ulnae), Boyer *et al*. (2010) confirmed that *Deccanolestes* was an arboreal mammal, but the morphology of the humerus is intermediate between

Cretaceous "condylarth" mammals and Cenozoic euarchontans. On the other hand, the humeri attributed to adapisoriculids were considered by them as morphologically intermediate between *Deccanolestes* and definitive Cenozoic euarchontans. This implies that *Deccanolestes* is more basal in position with respect to adapisoriculids and euarchontans. If *Deccanolestes* is accepted as a stem euarchontan, it has far reaching implications for the timing of origin and diversification of placental mammals. It would suggest that euarchontans and hence placental mammals originated before the K-Pg boundary in the Indian subcontinent, Africa or Europe. However, cladistic analysis carried out using both dental and postcranial characters revealed no close phylogenetic relationship between euarchontans and *Deccanolestes,* suggesting that the latter is not a Cretaceous placental mammal (Goswami *et al*., 2011). However, this analysis has demonstrated sister group relationship between *Deccanolestes* and African and European adapisoriculids and pushed them to a more basal position within the cladogram suggesting the existence of 30-45 m.y. ghost lineages for these Gondwanan eutherian mammals. Goswami *et al*. (2011) also supported faunal interchanges between India, Africa and Europe at or near the K-Pg boundary. Latest geometric morphometric study of the ankle bones of *Deccanolestes* showed that its astragalar morphology has no analogue in the extant mammalian species, but that this morphology was rather more common in the Cretaceous and Palaeocene eutherian mammals (Fabre *et al*., 2014).

A recent comparative study of faunal similarities or differences between the infratrappean and intertrappean beds has shown that the dinosaurs survived the early phase of volcanism though decreased in diversity and freshwater fauna was least affected by the initial volcanic eruptions (Prasad and Sahni, 2014). It was further observed that detritus-feeding freshwater vertebrate communities fared better than the terrestrial communities during the Deccan volcanism. As compared to dinosaur eggshells, the crocodilian and turtle eggshells are scarcely known from the Upper Cretaceous rocks of India. With the help of eggshell ultrastructure, Prasad *et al*. (2015) identified eggshells belonging to oofamilies Testudooolithidae and Krokolithidae in the vertebrate fauna of Kisalpuri intertrappean beds, Central India.

As compared to the extensive work carried out on the Upper Cretaceous infra- and intertrappean beds in the last three decades, vertebrate palaeontological research was initiated on the continental Upper Cretaceous Kallamedu Formation of Cauvery basin only recently. Prior to these recent studies, presence of fragmentary and poorly preserved dinosaur bones was noted by Matley (1929). The Kallamedu vertebrate fauna is not as diverse and abundant as that of the Deccan intertrappean beds, nevertheless added many new vertebrate groups to the Late Cretaceous vertebrate fossil list of India. The discovery of a troodontid dinosaur tooth from the Kallamedu Formation assumes great significance from palaeobiogeographic point of view. The presence of this typical Laurasian dinosaur in an essentially Gondwanan faunal assemblage at a time India was far to the south of Laurasian landmasses raises the question of whether troodontid dinosaurs migrated from Laurasia to India in the Late Cretaceous or this group was broadly distributed in the former Gondwanaland (Goswami*et al*., 2013). Prasad *et al*. (2013) described a vertebrate assemblage consisting of remains of fishes, amphibians, turtles, crocodiles and dinosaurs from the Kallamedu Formation. The dinosaur teeth representing abelisaurid dinosaurs seem to have a pan-Gondwanan distribution during the Cretaceous. The presence of *Simosuchus*-like notosuchian crocodile, the only known occurrence outside Madagascar, however, attests to a close biogeographic link between India and Madagascar in the Late Cretaceous (Maastrichtian). Very recently, Halliday *et al*. (2016) described phyllodontid fish *Egertonia*, a taxon with a primarily Laurasian distribution and only the second Cretaceous Gondwanan occurrence of this taxon from the Kallamedu Formation. Sister group relationships are known to exist between abelisaurid dinosaur fauna, bothremydid turtles, madtsoid and nigerophiid snakes, and gondwanathere mammals of India and Madagascar (see Prasad *et al*., 2013). *Simosuchus*-like crocodiles and *Egertonia* further add to the list of growing number of taxa common to Madagascar and India. Since India was separated from Madagascar by a wide ocean in the Late Cretaceous the common occurrence of closely related taxa raises the question on their evolution and dispersal in the Gondwanan continents. Future research should ascertain whether these common taxa were widely distributed in the former Gondwanaland and the latter's break-up led to the observed Late Cretaceous distribution under vicariant mode of evolution or whether there were some intermittent Late Cretaceous land bridges between India and Madagascar/South America.

Pre- and Post-collision Phase

Significant advances have been made during the past few years on the Eocene vertebrate faunas of India, especially mammals. These finds, documented mainly from the early Eocene Cambay Shale Formation of the well known Vastan Lignite Mine in District Surat (Gujarat), middle Eocene Harudi Formation of District Kutch (Gujarat), and from the Subathu Formation of NW Himalaya in the states of Jammu & Kashmir and Himachal Pradesh, testify to the importance of India as an important centre for the differentiation and dispersal of several major vertebrate groups. These finds also assume significance in the context of India's collision with Asia around the Paleocene-Eocene boundary and the resultant faunal exchanges with Eurasia (e.g. Bajpai, 2009).

Recently, the oldest South Asian tapiroid from India has been described by Kapur and Bajpai (2015a, b) from the early Eocene (~54-55 Ma) Cambay Shale at Vastan lignite mine, Gujarat. This new taxon (*Cambaylophus vastanensis*), which is based on a well preserved partial maxilla with molars and deciduous premolars, appears to show close phylogenetic relationships to the early Eocene tapiromorph *Gandheralophus* from Pakistan and is closely nested with the early Eocene (Bumbanian) tapiromorph *Orientolophus* from China. This new study clearly highlights the importance of *Cambaylophus* in evaluating the evolutionary relationships during the early radiation of tapiromorphs and suggests a degree of terrestrial connectivity between the Indian Subcontinent and the Asian landmass around the time of India–Asia collision, at or near the Paleocene–Eocene boundary (~55 Ma). Subsequently, Smith *et al*. (2015) also described a tapiroid from Vastan based on two isolated teeth, including a fragmentary premolar. Recent records of early Eocene mammals from Vastan also include a tillodont *Anthraconyx hypsomylus* that is interpreted to indicate Euroamerican affinities (Rose *et al*., 2013). Also reported recently (Rana *et al*., 2015) is the additional dental and postcranial material of *Indohyaenodon raoi*, the only known mammalian carnivore from Vastan which was originally described on the basis of several dentaries (Bajpai *et al*., 2009a).

Cooper *et al*. (2014), based on a detailed morphological and phylogenetic study, concluded that the anthracobunids, a long known group of ungulate mammals from the Indian subcontinent, are actually stem perissodactyls, the mammal order that includes modern horses and rhinos. Prior to this finding, anthracobunids were traditionally considered to be tethytheres, i.e. a group that is closely tied to the origin of elephants. Cooper *et al*.'s (2014) study is based on anthracobunid fossils comprising dental, cranial and postcranial remains including those from the Kalakot locality, Jammu & Kashmir. Interestingly, Cooper *et al*. (2014) reconfirmed that cambaytheres, a new family named and identified as perissodactyls by Bajpai *et al*. (2005), are a stem group to the mammal order Perissodactyla. In a similar finding, Rose *et al*. (2014) also favoured perissodactyl affinities of cambaytheres although they had initially disputed their assignment to Perissodactyla and instead referred them to tethyheres (anthracobunids). Cooper *et al*. (2014) also conducted studies on oxygen and carbon stable isotopes and the long bone geometries of the Eocene anthracobunids and cambaytheres and concluded that they fed on land but also spent time in the water, similar to modern rhinos. Overall, this new study has led to the identification of an Old World radiation of large, non-cursorial, partly aquatic perissodactyls that convergently came to occupy a basal tethythere-like niche on the northern coast of the Tethys Sea. The study not only expands our understanding of stem perissodactyl diversity but also lends support to the possible Out-of-India hypothesis for their origin.

Gupta and Kumar (2015) recently reviewed the Eocene rodent fauna of the Indian subcontinent and also described a small, new assemblage of early Eocene (late Ypresian) rodents from the type Subathu Formation, Himachal Pradesh, NW Himalaya. It is intriguing that ailuravine rodents (*Meldimys musak*), a European group purportedly recorded from the early Eocene Cambay Shale of Vastan mine (Rana *et al*. 2008) is completely absent from the nearly contemporary or slightly younger Himalayan Eocene assemblages. Furthermore, it is to be noted, as also suggested by Gupta and Kumar (2015), that *Meldimys musak* is hardly distinguishable from *Anthramys vastani* described as a ctenodactyloid (family indet.) by Bajpai *et al*. (2007) and that *M. musak* may turn out to be a junior synonym of the latter species.

Among the early Eocene lower vertebrate faunas from India, mention may be made of assemblages of frogs, lizards and birds from the Vastan section (Bajpai and Kapur, 2008; Prasad and Bajpai, 2008; Folie *et al*. 2013; Mayr *et al*. 2013; Rana *et al*. 2013). Folie *et al*.'s (2013) study of fossil frogs includes the families Pelobatidae and Rhacophoridae and compliments an earlier record of ranoid and discoglossid frogs from the same section by Bajpai and Kapur (2008). Paleobiogeographically, the presence of ranoids in Vastan supports an out-of-India dispersal pattern (Bajpai and Kapur, 2008). Overall, the anuran fauna from Vastan does not appear support faunal exchanges between India and Europe during the early Paleogene. Lizards in the Vastan fauna, represented mainly by the acrodontan agamids, suggest that some lineages may have been introduced into Laurasia from India, possibly during one of the several trans-Tethyan dispersal phases (Prasad and Bajpai, 2008). Additional acrodont lizards have since been described from Vastan by Rana *et al*. (2015). Also described recently from the early Eocene of Vastan are avian remains comprising several skeletal elements of the parrot-like bird *Vastanavis* with psittaciform affinities (Mayr *et al*. 2013).

The middle Eocene vertebrate record of the Indian subcontinent continues to provide critical insights into the origin of whales from a four-footed land animal (*Indohyus*), and this evolutionary change has now become one of the best understood examples of biological macroevolution that involved a drastic transition from land to sea. This major evolutionary event, which involved a number of organ systems, has been documented on the basis of a diverse assemblage of well preserved fossils discovered in the Eocene sections of Kutch (Gujarat) and the Himalayas (e.g. Thewissen*et al*. 2007; Bajpai *et al*. 2009b). In an important recent contribution (Cooper *et al*. 2012), a comparative morphological analysis of the postcranial elements of *Indohyus*, archaeocetes and extant artiodactyls, provides new insights into the aquatic and terrestrial locomotor affinities of the raoellid *Indohyus*, filling a critical gap in our understanding of the earliest part of the artiodactyl marine invasion. This study was based on over 200 postcranial fossils of *Indohyus* recovered from the Kalakot section of Jammu & Kashmir state. In another important work related to the evolutionary change from herbivory and omnivory to carnivory as reflected in the dental morphology, Thewissen *et al.* (2011) studied the wear facets, together with dental morphology and stable isotope ecology, across the artiodactyl-cetacean transition. This study found that the artiodactyls *Indohyus*, the closest known terrestrial relative of whales (Cetacea), had a tooth crown morphology very different from that of Eocene cetaceans, but with wear facets that are closer to those of Eocene cetaceans rather than to the facets of basal artiodactyls. This was a significant observation as it suggested that evolutionary changes in the masticatory function occurred prior to changes in crown morphology and diet at the origin of whales (Thewissen *et al*., 2011).

Younger and evidently more marine whales are known from the well dated middle Eocene (~ 42 Ma) rocks of Kutch, Gujarat. Recently, an excellently preserved skull of an archaic cetacean *Remingtonocetus harudiensis* from Kutch was described in considerable detail (Bajpai *et al*. 2011). This study, which also included reconstruction of the cranial cavity based on serial CT-scans, has significantly improved our understanding of the biology of remingtonocetids, a basal family of Eocene cetaceans that lived in muddy coastal, salt- or brackish water swamps of the Indian subcontinent. A recent study has also identified, for the first time, a diverse protocetid fauna from the middle Eocene of Kutch (Bajpai and Thewissen, 2014). The Kutch protocetids, which comprise a variety of genera (*Indocetus ramani, Babiacetus indicus, B. mishrai, Kharodacetus sahnii* and *Dhedacetus hyaeni)* with different ecological specializations, were rarer in abundance than the contemporaneous remingtonocetids. The protocetids fed higher up the food chain, although differences in tooth and jaw morphology and dental wear point to a range of diets and food processing abilities (Bajpai and Thewissen, 2014). Interestingly, *Kharodacetus* is the largest protocetid from Kutch and may have fed on the largest prey such as the catfish, crocodiles and remingtonocetid cetaceans.

In recent years, the subject of whale evolution has also been studied from a developmental perspective in conjunction with the fossil data. Unlike most mammals, precise occlusion has been secondarily lost in cetaceans, and their fossil record allows an understanding of the timing of the macroevolutionary events leading to their unusual dental morphology. In an important recent study (Armfield *et al*. 2013), it was suggested that a primitive pattern of rostral *Bmp4* and distal *Fgf8* expression across mammals was modified during cetacean evolution allowing a caudal expansion of *Bmp4* expression in the jaw that led to the extra teeth with simple, similar crowns seen in living toothed whales. These authors hypothesized that functional constraints underlying mammalian occlusion have been released in cetaceans, facilitating changes in the genetic control of early dental development.

Summary

The foregoing discussion on the vertebrate faunas of different phases of India's northward flight brings out clearly that during the pre-drift phase, as contrasted to previous works that focused mostly on non-dinosaurian reptilian fauna, the recent studies have substantially enhanced the diversity of dinosaur fauna from Upper Triassic and Lower Jurassic formations. Furthermore, this fauna suggests close biogeographic affinities with the Gondwanan continents and Europe. The first confirmed foot prints of dinosaurs were also documented from marine Jurassic rocks of Jaisalmer area. The fossil record of Jurassic mammals has also improved considerably with the discoveries of multituberculate, haramiyid, triconodont, symmetrodont, docodont and dryolestid mammals from the Kota Formation. Though these mammalian groups do not occur in great abundance, their diversity parallels that of the Laurasian continents. As compared to the fairly well documented fossil record of the pre-drift phase, the vertebrate fossil record for the early drift phase is very scanty, with only a few reports of shark remains coming from the marine Cretaceous sequences of the Cauvery basin.

The Late Drift and Pre-collision phases are the most extensively investigated time slices that attracted more attention because of their association with Cretaceous/Palaeogene (K/Pg) boundary mass extinction and the Palaeocene-Eocene Thermal Maxima (PETM), respectively. The Late Cretaceous fauna from the Deccan volcano-sedimentary sequences has been extensively studied in the last three decades as a consequence of which all the vertebrate groups with the exception of birds have been documented. Recent initiatives to unravel the vertebrate fauna of the Kallamedu Formation have also proved promising, with many new taxa being added to the Late Cretaceous faunal list from this formation. These studies have offered new insights into the mode of evolution of vertebrates during the physical isolation of India from all other landmasses. The common occurrence of bothremydid turtles, abelisaurid dinosaurs, notosuchian crocodiles and gondwanathere mammals in South America, Antarctica, Madagascar and India, and the close phylogenetic relationship between the representative species of these groups in India and Madagascar points to possible vicariant evolution of these groups following the break-up of former Gondwanaland. Furthermore, indigenous origination of certain groups, such as adapisoriculid mammals (*Deccanolestes*), and their subsequent dispersal to Africa and Europe has also been visualized (Prasad *et al*., 2010; Smith *et al*., 2010; Goswami *et al*., 2011).

Recent studies on stratigraphic units that correspond to pre-collision and post-collision phase, such as the Lower Eocene Cambay Shale of Vastan lignite mine, led to the discovery of the oldest Cenozoic vertebrate assemblage of South Asia. An exceptionally rich assemblage of mammals represented by more than 10 orders has been documented from this formation. Latest research has unambiguously shown that cambaytheres, the stem perissodactyls had originated in India. In addition to this, the oldest tapiroids and lagomorphs, and Gondwanan ranoid frogs and acrodont lizards which attest to 'out of India' dispersal hypothesis, have also been recorded from the Cambay Shale. From the Middle Eocene, the recent work on the transition from terrestrial to aquatic locomotion as well as on dental adaptations among raoellid artiodactyls and early cetaceans has significantly improved our understanding of early stages of whale evolution in the Indian subcontinent. Efforts are also being made to understand whale evolution in a developmental (*evo-devo*) perspective.

Concluding Remarks

Summing up, significant advances have been made in recent years to understand the vertebrate evolution in India in a plate tectonic framework, particularly from the Upper Cretaceous and Eocene deposits of India. This research needs to be undertaken more vigorously in future as it is expected to throw up many new questions and surprises from time to time that will have an important bearing on our understanding of the origin, evolution and dispersal of the various groups of vertebrates. Furthermore, it is important to fill the existing gaps in the vertebrate record, specifically from the Palaeocene which is a critical period for a better understanding of the evolutionary trajectories from the Cretaceous to the Eocene.

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