India as a “Noah’s Ark” before collision with Eurasia: Paleoenvironment and paleobiogeography of the continental early Eocene vertebrate fauna of Gujarat

by

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KEYWORDS. — India, Eocene, vertebrate paleontology, paleogeography, paleoenvironment.

SUMMARY. — For the past twenty years, an Indian-American-Belgian team has carried out twelve seasons of collaborative field work in search of vertebrates from the Cambay Formation in lignite mines of Gujarat, western India. Here I summarize our principal discoveries in the Vastan, Mangrol, and Tadkeshwar mines, including an updated overview of the whole vertebrate fauna. The fauna is around 54.5 million years old, representing tropical rainforest conditions in a coastal brackish paleoenvironment. It includes the earliest modern mammals from the Indian subcontinent as well as endemic taxa. The most important result at the paleobiogeographical level is discovery of several vertebrate taxa of Gondwanan affinities, indicating that the early Eocene was a crucial period in India when Laurasian taxa with western European affinities co-existed with relict taxa from Gondwana before the actual collision of India and Eurasia. Terrestrial faunas could have dispersed to or from Europe when the Indian subcontinent contacted, episodically, different island blocks, such as the Kohistan-Ladakh island-arc system, along the northern margin of Neotethys Ocean.

MOTS-CLÉS. — Inde, Eocène, paléontologie des vertébrés, paléogéographie, paléoenvironnement.

RÉSUMÉ. — *L'Inde vue comme une "arche de Noé" avant la collision avec l'Eurasie : Paléoenvironnement et paléobiogéographie de la faune de vertébrés continentale de l'Éocène inférieur du Gujarat.* — Au cours des vingt dernières années, une équipe indo-américano-belge a mené douze campagnes de terrain à la recherche des vertébrés de la Formation de Cambay dans les mines de lignite du Gujarat, dans l'ouest de l'Inde. Je résume ici nos principales découvertes dans les mines de Vastan, Mangrol et Tadkeshwar, et fournis un aperçu actualisé de l'ensemble de la faune de vertébrés. La faune date d'environ 54,5 millions d'années et témoigne de conditions de forêt tropicale humide dans un paléoenvironnement côtier saumâtre. Elle comprend les premiers mammifères modernes du sous-continent indien ainsi que des taxons endémiques. Le résultat le plus important au niveau paléobiogéographique est la découverte de plusieurs taxons de vertébrés d'affinités gondwaniennes, ce qui indique que l'Éocène inférieur a été une période cruciale en Inde où des taxons laurasiens d'affinités ouest-européennes ont coexisté avec des taxons reliques du Gondwana avant la collision réelle de l'Inde et de l'Eurasie. Les faunes terrestres ont pu se disperser vers ou depuis l'Europe lorsque le sous-continent indien est entré en contact, de manière épisodique, avec différents blocs insulaires, tels que le système d'arcs insulaires Kohistan-Ladakh, le long de la marge septentrionale de l'océan Néotéthys.

TREFWOORDEN. — India, Eoceen, vertebraten paleontologie, paleogeografie, paleomilieu.

SAMENVATTING. — *India als "Ark van Noach" voor de botsing met Eurazië: Paleomilieu en paleobiogeografie van de continentale Vroeg-Eocene vertebratenfauna van Gujarat.* — De afgelopen twintig jaar heeft een Indiaas-Amerikaans-Belgisch team twaalf seizoenen lang gezamenlijk veldwerk verricht op zoek naar vertebraten van de Cambay Formatie in bruinkoolmijnen van Gujarat, in het westen van India. Hier vat ik onze belangrijkste ontdekkingen in de Vastan, Mangrol en Tadkeshwar mijnen samen en geef ik een actueel overzicht van de vertebratenfauna. De fauna is ongeveer 54,5 miljoen jaar oud en vertegenwoordigt tropisch regenwoud in een brak kustmilieu. Het omvat de vroegste moderne zoogdieren van het Indiase subcontinent evenals endemische taxa. Het belangrijkste resultaat op paleobiogeografisch niveau is de ontdekking van verschillende vertebraten taxa met verwantschap met Gondwana, wat erop wijst dat het Vroeg-Eoceen een cruciale periode in India was waarin Laurasische taxa met West-Europese verwantschap naast relict taxa uit Gondwana bestonden voordat India en Eurazië daadwerkelijk met elkaar in botsing kwamen. Terrestrische faunas kunnen zich hebben verspreid naar of vanuit Europa toen het Indiase subcontinent episodisch in contact kwam met verschillende eilandblokken, zoals het Kohistan-Ladakh eiland-boogsysteem, langs de noordelijke rand van de Neotethys Oceaan.

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1. Introduction

The Indian subcontinent underwent a long voyage northward after its breakup from the Gondwana landmass and remained for a long period of time drifting in isolation from other landmasses before its collision with Asia. The understanding of the timing and sequence of this almost 9000 km voyage in 160 million years (My) made important progress since the first attempt of Wegener (1912) to connect India with widely separated landmasses of the Southern Hemisphere. The continental drift theory of Wegener (1912) has been based on paleontological record with common terrestrial vertebrates and plants present in the widely dispersed Gondwana continents (Fig. 1; see Chatterjee *et al*., 2017 for an overview). During this long journey, the Indian subcontinent separated from the last two Gondwana landmasses, Madagascar and the Seychelles, at the Coniacian, 88 My ago and early Paleocene, 64 My ago respectively (Storey *et al*., 1995; Chatterjee *et al*., 2013). This period of time is highlighted by several latest Cretaceous Madagascar terrestrial vertebrate taxa, which have sister-taxon relationships to Campanian/Maastrichtian (83-66 My ago) taxa of both the Indian subcontinent and South America, revealing long ghost lineages (see Ali & Krause, 2011 for an overview).

On another note, the timing of the initial collision of the Indian subcontinent with the Asian continent has been strongly debated and is now situated during the early Eocene at ca. 50 My ago (Jagoutz *et al*., 2015) or ca. 55 My ago (Zhu *et al*., 2015; Ding *et al*., 2016) or even already in the Paleocene at ca. 59 My ago (Hu *et al*., 2015) or ca. 61 My ago (An *et al*., 2021; Yuan *et al*., 2022), depending on the method to constrain the timing of collision onset and the different definitions of the collision onset (Hu *et al*., 2016).

The stages between the initial and terminal phases of a collision event are summarized here for ease of understanding. Convergence between plates initially involves the oceanic crust (lithospheric mantle) and does not bring continental crusts into direct contact. The heavy oceanic crust is subducted, and it is only in a relatively later phase of convergence that the light continental masses and their shallow marine margins come into contact, allowing potential contacts and exchanges between faunal stocks. This occurs before orogenic uplifts and the formation of mountain ranges (the Himalayan range in this case).

It seems now well accepted that the collisional events began with the collision of India and a Trans-Tethyan subduction zone, followed by the collision of India (plus Trans-Tethyan ophiolites) with Eurasia (Martin *et al*., 2020). This model with a double subduction implies that the part of the vanished continent that has been subducted and compressed since the India-Asia collision, called Greater India, was smaller than previously estimated and that the terminal collision between India and Asia occurred at ca. 50 Ma, followed by the quasi-synchronously closing of the Neotethys Ocean (Jin et al., 2023). Furthermore, initial collision was not necessarily coincident with subaerial contact with Asia. The Neotethys, which persisted for some time between India and Asia, must have represented a barrier to dispersal before its closure and exchanges of Indian and Asian faunas (Krause & Maas, 1990; Macey *et al*., 2000; Bossuyt & Milinkovitch, 2001; Conti *et al*., 2002; Chatterjee *et al*., 2013). The rich middle Eocene vertebrate faunas from the Subathu Formation of the Kalakot area, Jammu and Kashmir, India and the Kuldana Formation in Punjab and Khyber Pakhtunkhwa, Pakistan illustrate well the Asian affinities of the Indian subcontinent faunas around 48-49 My ago with the presence of brontotheriid and hyracodontid perissodactyls, as well as ctenodactyloid rodents (Kumar & Sahni 1985; Thewissen *et al.*, 1987; Kumar *et al.*, 1997; Thewissen *et al.*, 2001).

However, there is a gap of about 20 million years in the knowledge of Indian faunas between the latest Cretaceous and the middle Eocene. So, what were the Paleocene and early Eocene terrestrial vertebrate faunas in India before the so-called “Noah’s Ark” (McKenna, 1973) collided with Eurasia (Fig. 2)? To answer that important question 12 fieldwork missions were organized in the early Paleogene of western India by our Indian-American-Belgian team between 2004 and 2020. Here I report on the main scientific achievements and fossil discoveries that have been made.

2. The discovery of the earliest modern mammals from the Indian sub-continent

2.1. Origin of the expeditions

In February 2001, with the support of a grant from the National Geographic Society, a team led by Kenneth D. Rose from John’s Hopkins University, Baltimore and Ashok Sahni from Panjab University, Chandigarh began a search for early Cenozoic mammals in several lignite mines of western Rajasthan. The team did not succeed in finding mammals in Rajasthan, but in the Akli Formation at Giral Mine and Kapurdi Formation at Barakha fuller’s earth Mine near Barmer they did discover diverse late Paleocene-early Eocene marine vertebrate assemblages of sharks, rays, and bony fishes (Rana *et al*., 2005, 2006). On the proposal of K. D. Rose, I continued the prospection in western India with Pieter Missiaen from University of Ghent and joined, in November 2004 an Indian team for exploring the Vastan Lignite Mine, one of the numerous lignite mines of Gujarat (Fig. 3). The Vastan Lignite Mine was a large open cast mine of about 2.0 km long on 1.5 km wide and 130 m deep, located on the northwestern border of the main Deccan Traps province. The Deccan Traps were sometime exposed in the mine and limited the mining operation (Fig. 4a-b). The Indian team was leaded by Ashok Sahni and composed by Neera Sahni (Panjab University, Chandigarh), Pratul K. Saraswati (IIT, Bombay) and Rajendra S. Rana, Hukam Singh and one student (H.N.B. Garhwal University, Srinagar). The purpose of the mission was to collect vertebrate remains by screen washing because Rajendra S. Rana and Hukam Singh found numerous shark and ray teeth in different levels of the Cambay Formation of Vastan mine (Rana *et al*., 2004; Sahni *et al.*, 2006). Among the vertebrate discoveries were also four small, isolated teeth of terrestrial mammals, including two bat molars which were all found “near the base of the section overlying a thin lignite bed in a grayish green clay deposit” (Rana *et al*., 2005).

Fieldwork at Vastan mine started on November 16th, 2004, and the grayish green clay deposit was quickly located. At the end of the first day, after digging in difficult condition the grey sticky clay with hammers, we asked assistance from a mine operator to dig the overlying layers with a bulldozer. The morning of November 17th, when cleaning all the big blocks of sediment which fell on the grey clay, we observed a thin organic-rich lens of maximum 30 cm thick and about 5 m long just above the clay layer (Fig. 5a). This lens was very rich in small fish bones. After five minutes searching at the surface of the lens, a mammal incisor the size of a human incisor was discovered just above the contact between the terrestrial bone-bearing lens and the clay layer below (Fig. 5b). Thirty minutes later, a mammal maxillary with four teeth was discovered (Fig. 5c-d; Rose *et al*., 2006, fig. 3B-E). Again, the teeth had similar size to those of a human being. By this way, the first fossils of the now classic mammal species *Cambaytherium thewissi* were discovered. It was the organic-rich lens which was at the origin of the terrestrial Vastan fauna and not the grey clay layer.

On November 19th, the work started for digging the fossil lens and collecting and drying the sediment. At the end of day of November 20th, the residue of the first screen washing was still drying on plastic sheets in the sunset when a first small mammal jaw with four teeth was found; it became later the holotype of the primate *Asiadapis cambayensis*, type-species of the family Asiadapidae (Rose *et al*., 2007, 2009). The sorting of the residue in Brussels and the study of the material in Brussels and Baltimore during the first semester 2005 led to a first paper about this early Eocene continental vertebrate assemblage, including the earliest modern mammals of the Indian subcontinent (Rose *et al*., 2006).

2.2. 12 EXPEDITIONS IN 16 YEARS

Following the success of the 2004 field mission, eleven other paleontological expeditions were organized in the lignite mines of Gujarat. The National Geographic Society funded the expeditions in Vastan mine in 2006, 2008, 2011, and 2012, and in the ephemeral mine of Mangrol in 2013. Vastan mine closed in 2013. The first terrestrial vertebrates of Tadkeshwar mine were discovered by R. S. Rana and Kishor Kumar from the Wadia Institute for Himalayan Geology during a reconnaissance in 2014. Fieldwork in Tadkeshwar in 2015, 2016, 2017, 2018, 2019, and 2020 (Fig. 4c) were funded by the Leakey Foundation and the Belgian Science Policy Office. In March 2020, the expedition was suddenly interrupted by the Corona virus pandemic and the American and Belgian members of the team had to leave India in an emergency.

3. Geological settings and collecting techniques

Terrestrial vertebrates collected at Vastan, Mangrol and Tadkeshwar mines all came from the early Eocene Cambay Formation, a lignite-bearing sequence, which was deposited in the intra-cratonic graben of the Cambay Basin, a major hydrocarbon source rock in western India (Sahni *et al*., 2006). The Cambay Basin is a narrow, elongated rift graben extending from the Surat area in the south to Sanchor area in the north of Gujarat, and continuing northwards into the Barmer Basin of Rajasthan (Mathur *et al*., 1968). In Vastan mine, the deposits of the Cambay Formation corresponded to a relatively low-energy shallow bay flanked landward by a salty, brackish to freshwater marsh complex; the marshland was cut by freshwater or tidal channels (Prasad *et al*., 2013). Mangrol mine was an ephemeral mine nearly adjacent to Vastan mine and with a similar stratigraphic sequence. Tadkeshwar mine was similar to Vastan and Mangrol, the major difference being the presence of intercalated erosional sandy channels at Tadkeshwar, which were absent from the Vastan succession (Smith *et al*., 2016). Lignite layers at Vastan as well as at Tadkeshwar were characterized by pollen belonging to the lowland tropical rainforest dominated by the Dipterocarpaceae while shale horizons contained abundant mangrove pollen (Prasad *et al*., 2013; Rao *et al*., 2013; Singh *et al*., 2014).

The three mines were a real paradise for paleontologists and geologists because they contained fossils in almost all the layers and the diversity of taxonomical groups was astonishingly high: vertebrates, mollusks, insects and arachnomorphs in amber, leaves, seeds and fruits, pollen, dinoflagellates, foraminifera… The terrestrial vertebrate remains were stratigraphically more restricted than most other fossil groups and, in the three mines, were generally concentrated in lenses representing a very local environment, except for Tadkeshwar mine, where they were also present in channels that gathered remains from a wider environment (Smith *et al*., 2016).

The age of the terrestrial vertebrates from the Cambay Formation has been estimated to date from ca. 54.5 Ma, corresponding to the early Ypresian, based on a consensus established from the results provided by foraminiferans, dinoflagellate cysts, pollen, nannofossils, dispersed organic carbon (d13C) and strontium isotopes. However, the precise age of the vertebrate fauna remains uncertain because the ages of the foraminiferans and dinoflagellate cysts are themselves approximations and the various isotope studies are in conflict (see Smith et al. 2016 for a synthesis).

Two different collecting techniques were developed to sample large vertebrates as well as microvertebrates in order to obtain the most complete vertebrate assemblage. Larger specimens were exposed on the surface of fossil-bearing lenses and channels by quarrying with icepicks (Fig. 6). Sediment was also collected from the same lenses and channels for screen-washing. This involved drying sediment on tarps, then dissolving in buckets of water and screen-washing at the bottom of the mine (Fig. 7). Screen meshes of 5 mm and 1 mm were used. The fossils were picked out from the washed residue in the laboratory. Most of the collected vertebrate remains were covered with the acrylic resin paraloid B72 (ethyl-methacrylate copolymer) against development of pyrite and other specimen alterations.

4. The continental vertebrate fauna

The discovery of early Eocene vertebrates and especially mammals in India is of particular interest in the context of research focused on the origin of modern vertebrate faunas appearing at the earliest Eocene, 56 My ago (see Smith *et al*., 2013 for a summary). In this framework, I present here an updated faunal inventory of the early Eocene continental vertebrates from the Cambay Formation (Table 1). Based on the geological setting, this vertebrate assemblage comes from fresh and brackish water deposits represented by lenticular layers and channels. Therefore, this inventory does not include the typical marine fish discovered in marine layers of the same formation (see Rana *et al*., 2004; Nolf *et al*., 2006; Rose *et al*., 2020, table 2 for an exhaustive list).

At first glance, the continental fauna from the Gujarat lignite mines seems relatively similar in composition to other early Eocene vertebrate faunas such as they are known from North America, Europe and Asia. Several modern vertebrate taxa of the Cambay Formation are present together with archaic taxa, including endemic taxa. Among the modern taxa are bombinatorid and ranid frogs, caenophidian snakes and numerous mammals such as ischyromyoid rodents, a lagomorph, adapiform and omomyid primates, a hyaenodontan, bats, tapiroid perissodactyls and diacodexeid artiodactyls. The cosmopolitan archaic taxa are a coryphodontid, estonychid tillodonts, and an apatemyid. The endemic archaic taxa are represented by several mammals of uncertain affinities, cimolestans and anthracobunians. However, when comparing more in detail with the other early Eocene vertebrate faunas from the Northern Hemisphere, the Indian fauna appears somewhat taxonomically unbalanced and present some distinctions.

5. Paleoecological specificities

5.1. Fishes

Fish remains are the most abundant vertebrate specimens found in the continental layers of the Cambay Formation. Most of them are isolated bones of bony fishes difficult to identify below the familial level (Table 1). Among the fish, the most remarkable and intriguing species was probably *Avitoplectus molaris*, a gymnodont tetraodontiform found in Tadkeshwar mine and represented by fused lower jaws like those in the living porcupinefish (*Diodon*), burrfish (*Chilomycterus*), and sunfish (*Mola*) (Smith *et al*., 2016). The unique morphology of this jaw, which bears molariform teeth, has led to the erection of the new family Avitoplectidae (Bemis *et al*., 2017).

Curiously, elasmobranch teeth were also found with continental vertebrate remains in all the excavated lenses and channels. Although frequent, their diversity is very low. They belong to eagle rays (*Myliobatis* spp.) and stingrays (*Dasyatis* spp.). Sharks are represented by the small extinct carcharhinid *Physogaleus* sp., a taxon with teeth similar, although smaller, to those of the living tiger shark. Today, some euryhaline species of sharks (e.g., sawfishes *Pristis pristis*, whaler sharks *Carcharhinus* spp. And river shark *Glyphis* sp.) and rays (e.g., dasyatid stingrays and the skate *Zearaja maugeana*), are known to live in estuarine/brackish water and to enter rivers, some being obligate freshwater elasmobranchs such as potamotrygonid stingrays (Lucifora *et al.*, 2015). Stingrays have even been described from the early Eocene freshwater Green River Formation, Wyoming (Carvalho *et al*., 2004). So, the fish composition of the continental deposits of the Cambay Formation suggests a brackish to freshwater paleoenvironment.

5.2. Amphibians

Among the specificities of the Indian faunas are the absence of caudates (e.g., salamanders). However, amphibians are represented by at least four anurans from four different families identified on basis of hundreds of specimens, mainly ilia and vertebrae (Folie *et al*., 2013; Smith *et al*., 2016). The frogs are of particular interest at taxonomical level. The most abundant species, *Eobarbourula delfinoi* represents the oldest record of the Bombinatoridae and might have been capable of displaying the Unken reflex (defensive posture of an animal achieved by turning its body upside down to reveal its brightly colored ventral side in order to deter a predator from attacking) based on the morphology of its vertebrae (Folie *et al*., 2013). Another abundant taxon is a ranoid frog, possibly being the oldest true ranid.

5.3. Turtles

Turtles are relatively rare and known only from fragmentary material (Smith *et al*., 2016). One pleurodire (side-necked turtle) taxon of the hyperfamily Pelomedusoides, the most diverse group, possibly a bothremydid, is evidenced by fragments from the plastron and the carapace. Cryptodires (hidden-necked turtles) are represented by two trionychians: a carettochelyid (the only single living species is the pig-nosed turtle *Carettochelys insculpta*) and a true trionychid (soft-shelled turtle).

5.4. Squamates

Another paleoecological curiosity is among the lizards (Lacertilia). They are represented by a nice diversity of acrodont lizards: four agamids and one priscagamid (Rana *et al*., 2013). They are also diversified at the dental morphology level with dentitions varying from slightly heterodont in *Vastanagama* and *Indianagama* to very heterodont in *Heterodontagama* and *Tinosaurus*. All the other early Eocene contemporaneous lizard families are absent. This is surprising because the diversity of lizards during the very warm early Eocene is generally high on other continents. Typical groups such as gekkotans, scincomorphs, lacertids, amphisbaenians, anguimorphs, including varanids, and iguanids, are absent. This may explain why the Indian acrodontans are so morphologically diverse, probably occupying different ecological niches.

Regarding the snakes, the situation is very different, and their diversity in terms of taxonomic groups is very high. Small caenophidians, including early colubroid-like snakes, are abundant and diversified (Rage *et al*., 2008). The recent revision of one of them, *Thaumastophis missiaeni*, allowed to define the new family Thaumastophiidae (Zaher *et al*., 2021). The palaeophiid aquatic snake *Palaeophis vastaniensis* is the most abundant snake. Boids and russellophiids are moderately represented. Madtsoiids are also present, including the giant species *Platyspondylophis tadkeshwarensis*, which presents burrowing features, suggesting that it was fossorial and capable of extensive lateral mobility (Smith *et al*., 2016). Due to its very large size, it was probably able to burrow under mats of vegetation with a behavior similar to the living anaconda *Eunectes*.

5.5. Crocodylomorphs

Remains of crocodylomorphs are rare in the Cambay Formation, whereas they are sometime very abundant in early Eocene vertebrate localities of other continents. Only one taxon has been referred to a dyrosaurid neosuchian based on a coracoid bone from Tadkeshwar mine (Smith *et al*., 2016). However, the morphology of the teeth discovered in the same stratigraphic level is more suggestive of a sebecosuchian notosuchian. In any case, no modern crocodilian (Eusuchia) has been recorded at the moment in the Cambay Formation, whereas eusuchians are known since the Cretaceous on other continents (Rio & Mannion, 2021).

5.6. Birds

Bird remains are not rare in the Cambay Formation. However, they are not diverse and most of them belong to the endemic family Vastanavidae, a group that is close to the late Eocene Quercypsittidae known from Europe (Mayr *et al*., 2010, 2013). Interestingly, vastanavids had semi-zygodactyl feet (i.e., the fourth toe was spread laterally if not completely reversed) with short tarsometatarsus and are considered as a stem group of the parrots (Psittaciformes). These features indicate that *Vastanavis* was an arboreal bird, and its abundance in the locality suggests a forested paleoenvironment (Mayr *et al*., 2010).

5.7. MAMMALS

The composition of the mammal fauna from the Cambay Formation is very informative. Before analyzing its specificities, it is worth noting that the mammal *Indodelphis luoi*, based on a single lower molar from Vastan and referred to a peradectine metatherian by some morphological similarities with didelphid marsupials (Bajpai *et al*., 2005a), is here provisionally transferred to the adapisoriculid mammals. This molar indeed does not present the classic characters of Paleogene metatherians but resembles a m1 of an adapisoriculid of *Afrodon* type, with similar proportions to the somewhat larger species *A. gheerbranti* (De Bast *et al*., 2012, fig. 2E). Similarly, the insectivore-like mammal *Indonyctia cambayensis* has been referred to the family Nyctitheriidae, based on two partial dentaries described as similar to the dentary of the asionyctiine *Voltaia* (Das *et al*., 2021). The authors made their identification based on five dental characters mentioned as unambiguous synapomorphies in the cladistic analysis of Manz and Bloch (2015). These characters may indeed be considered as diagnostic of nyctitheriids but only by comparison with the outgroups considered in Manz and Bloch's analysis, which are the cimolestid *Maelestes gobiensis*, the erinaceomorphs *Macrocranion junnei* and *Adunator minutus*, and the closest taxon to nyctitheriids "*Wyonycteris*" *microtis*. The analysis of Manz and Bloch (2015) was not performed to discriminate different families of insectivore-like mammals but to discriminate the species and genera inside the clade Nyctitheriidae. In my point of view, *Indonyctia cambayensis* is not a nyctitheriid but a cimolestan mammal, maybe belonging to the family Cimolestidae. Typical characters of *Indonyctia*, which are not present in nyctitheriids are the important diastema between p3 and p4, the very simple shape and rounded occlusal outline of p4, the very large single-rooted p2, and the strong curved shape of the dentary basis. None of these characters correspond to nyctitheriids, especially not to asionyctiines (Missiaen & Smith, 2005; Lopatin 2006).

The first specificity is that there is only one predator in the fauna, *Indohyaenodon raoi* (Bajpai *et al*., 2009; Rana *et al*., 2015). This medium-sized mammal belongs to the Hyaenodonta, a typical group of carnivorous mammals with three carnassial molars per hemimandible. True carnivoran mammals are absent from the early and middle Eocene of India whereas they are present at the same period in North America, Europe and Asia.

Arboreal mammals are well represented and include at least the hyaenodontan, rodents, primates, bats and an apatemyid. However, their composition is also particular. Only one rodent species, '*Meldimys*' *musak,* has been formally identified whereas rodents are often the most diversified mammal group in early Eocene faunas (Rana *et al*., 2008). '*Meldimys*' *musak* was considered as an ailuravine ischyromyoid rodent, a subfamily only known from Europe and North America while it has recently been placed as the sister species of the basal Theridomorpha (Vianey-Liaud & Marivaux, 2021). Small adapoid primates of the family Asiadapidae with a primitive dental morphology are frequent while omomyids, although present, are rare (Bajpai *et al*., 2005c; Rose *et al*., 2007, 2009a, 2009b, 2018). Very well-preserved limb bones of these Indian primates revealed more primitive postcranial characteristics than have been previously documented, making these primates the most primitive known remnants of the divergence between strepsirrhine and haplorhine primates (Dunn *et al*., 2016). Bats are especially abundant and diversified. At least eight species are present, which belong to five families. Four of these families are basal and became extinct by the end of the middle Eocene (Smith *et al*., 2012; Gunnell *et al*., 2017).

Ungulates are known from numerous dental and postcranial remains of the cosmopolitan basal artiodactyl *Diacodexis* (Kumar *et al*., 2010) and the endemic anthracobunian *Cambaytherium* (Bajpai *et al*., 2005b, 2006; Rose *et al*., 2006; Smith *et al*., 2016). The latter has been shown as the sister group of perissodactyls (Rose *et al*., 2014, 2020). True perissodactyls are represented only by two tapiroids, which are rare (Kapur & Bajpai, 2015, Smith *et al*., 2015). No equoid has been discovered up to now whereas this group is present and sometime frequent in the early Eocene of Europe and North America (Hooker, 1994; Gingerich, 1991; Rose, 2006).

5.8. Paleoenvironment

The distinction of the Indian vertebrate faunas might be explained by a particular paleoenvironment. Fossil fruits, seeds and leaves identified in the Gujarat lignite mines indicate a tropical deciduous forest with moisture loving plants as in southern India today. The pollen is characteristic of mangrove and tropical rain forest (Prasad et al., 2013). Several elements of the fauna and flora indicate a coastal environment with brackish water. This environment seems therefore relatively unique by comparison with other early Eocene faunas known on other continents of the northern hemisphere. However, the middle Eocene vertebrate faunas from the sub-Himalayas in the area of Kalakot (Subathu Group, Jammu and Kashmir), which represent a different type of deposit than in the Gujarat, share the presence of hyaenodontans whereas true carnivorans are also absent. This absence of carnivorans is similarly observed in Eocene Pakistan fossil localities (Gingerich *et al*., 2001) but we cannot totally exclude that this absence results from an insufficient sampling (Chatterjee *et al*., 2017, p. 98). In any case, similarities between India and Pakistan vertebrate compositions seem in favor of a paleobiogeographic cause to explain the distinction of the vertebrate assemblage from the Indian subcontinent.

6. Paleobiogeographic specificities

6.1. Gondwanan affinities before the continental early Eocene Gujarat faunas

The latest Cretaceous mammals from India, which are also the oldest of the Indian sub-continent, are only known by a few isolated teeth and postcranial elements from Deccan intertrappean beds. These fossil remains indicate the presence of two allotherian mammals, represented by a gondwanathere and a possible haramiyidan, and two eutherian mammal groups, represented by adapisoriculids and a condylarth (Anantharaman *et al*., 2006; Prasad *et al*., 2007, 2010; Wilson *et al*., 2007). The mammals mostly represent Gondwanan elements suggesting their African affinities. Among them, only the adapisoriculids indicate Euro-African affinities (Prasad *et al*., 2010; Smith *et al*., 2010). Adapisoriculids are indeed already present on the European continent since the early Paleocene with at least five species described from Hainin in Belgium (De Bast *et al*., 2012; De Bast & Smith, 2017).

6.2. Asian affinities after the continental early Eocene Gujarat faunas

The early Eocene vertebrate faunas from the Gujarat lignite mines are important because no continental vertebrate fauna has been discovered yet in the Paleocene of India. Moreover, until the discovery of Vastan continental layers in 2004, the oldest Cenozoic terrestrial vertebrate faunas from the Indian subcontinent were those from the early Lutetian of the Subathu Formation in India and Kuldana Formation in Pakistan, the late Ypresian of the Upper Ghazij Formation in Balochistan, Pakistan and early or middle Ypresian of the middle Ghazij Formation in Pakistan. The latter fauna has yielded only endemic mammals such as the quettacyonid condylarths *Quettacyon*, *Machocyon*, *Sororocyon* and *Obashtakaia* (Gingerich *et al.*, 1997, 1998, 1999, 2001) and the cambaytheriid *Nakusia* (Ginsburg *et al.*, 1999). However, the former faunas show already important Asian affinities with several groups shared with Chinese faunas (e.g., ctenodactyloid rodents, raoellid and dichobunid artiodactyls, isectolophid, lophialetid, eomoropid, hyracodontid and brontotheriid perissodactyls; Gingerich *et al*., 2001; Thewissen *et al*., 1987, 2001; Missiaen *et al*., 2011; Missiaen & Gingerich, 2012, 2014). Later, ctenodactyloid rodents have also been described from the late early Eocene part of the Subathu Formation in Himachal Pradesh, India (Gupta & Kumar, 2015), suggesting that the Neotethys was already closed after the early Eocene and that dispersals were already effective (Chatterjee *et al*., 2013).

6.3. European affinities with a few Gondwanan relict taxa in the continental early Eocene Gujarat faunas

The early Eocene vertebrate faunas from Vastan and Tadkeshwar are clearly distinct from the middle Eocene faunas and seem to represent the time period just before the India-Asia collision and have revealed unexpected affinities with Europe (see Smith *et al*., 2016). One might think that this period of isolation in the Indian ocean would have produced an endemic fauna with African origins. This would be logical considering the geographic origin of the subcontinent. But the discovery of the early Eocene faunas from the Gujarat lignite mines has revealed little endemism, leading Chatterjee *et al*. (2017, p.7, p.73) to qualify the paleobiogeographic scenario of Krause & Maas (1990) and to suggest that India was not a standard “Noah’s Ark” isolated from adjacent landmasses by oceanic barriers. These authors rather regard India like a “passenger ship with a mobile gangplank” connected to the Oman-Kohistan-Ladakh arc, serving as a filter bridge that permitted faunal interchange from one continent to another as India moved northward across the Neotethys during the Paleocene and early Eocene.

Although their paleobiogeography is related to Western Europe and not directly to Africa and/or Asia (=Laurasian taxa of European affinities), the Vastan and Tadkeshwar faunas kept a few relict taxa from Gondwana, which seem to have persisted until the early Eocene. This is the case of the Pelomedusoides-group turtle, the giant madtsoiid snake and the crocodylomorph. The geographic origin of the adapisoriculid mammals *Bharatlestes kalamensis* and *Indodelphis luoi* is more difficult to establish because adapisoriculids are already present and diversified during the latest Cretaceous in India and Paleocene in Europe and North Africa (Gheerbrant *et al*., 1998; Smith *et al.*, 2010; Prasad, 2012; De Bast *et al*., 2012).

Some other taxa were new to science and have been described for the first time from the Gujarat lignite mines and therefore can be seen as endemic taxa until proven otherwise. This is the case of avitoplectid fish, vastanavid birds, anthracobunian ungulates, the hyracoid-like *Pahelia mysteriosa*, and possibly vastanid insectivores. The most emblematic anthracobunian ungulate from India is *Cambaytherium*. *Perissobune* from the early Eocene of Pakistan (Missiaen & Gingerich 2014) is included in cambaytheriids and therefore suggests that this family is endemic to the Indian sub-continent. Although the origin of cambaytheriids is still unknown, their discovery and phylogenetic relationships suggest that perissodactyls originated on the Indian subcontinent.

Among the numerous vertebrate groups of European affinities, some are also distinctive at paleogeographic level. A peculiarity of the vertebrate assemblage from the Gujarat lignite mines is the absence of all the lizard groups except acrodontans. Although hyaenodontans are present in the early Eocene of Europe, North America and Asia, the Indian hyaenodontans seem not directly related to any of them. *Indohyaenodon* from Vastan and Tadkeshwar is indeed retrieved with other South Asian hyaenodontids as a stem group that includes most African hyaenodontids (Rana *et al*., 2015). Interestingly, carnivorans are also absent from Africa, where hyaenodontans have been reported since the Paleocene (Gheerbrant *et al*., 2006; Solé *et al*., 2009).

The diversity of Indian bats is higher than anywhere else with four families shared with western Europe. At generic level, *Icaronycteris*, *Hassianycteris*, and probably *Archaeonycteris* are in common between India and Europe. But other genera are known only from India (e.g., *Protonycteris*, *Cambaya*, *Jaegeria*), suggesting a possible paleogeographic origin of bats on the Indian sub-continent. The Vastan and Tadkeshwar bats exhibit very primitive dental morphology suggesting that Indo-Pakistan potentially could be the source area for the initial radiation of bats (Smith *et al*., 2012).

6.4. No Asian affinities in the continental early Eocene Gujarat faunas

Recently, Kapur *et al*. (2022) suggested Asian affinities for some of the Vastan and Tadkeshwar mammals, namely lagomorphs, the insectivore *Indonyctia* and tapiromorph perissodactyls. The authors consider these three taxa to be evidence of significant faunal exchanges between India and Asia at or before the Paleocene-Eocene boundary, ca. 56 My ago, implying an initial contact between the two landmasses at this time. Although these three groups are indeed present in Asia at a given time, they do not suggest exchanges between India and Asia at or near the Paleocene-Eocene boundary. Here I develop the reasons why these three Indian taxa do not support such a hypothesis.

The lagomorph fossils are four typical gracile footbones (calcanei and astragali) showing a mosaic of derived cursorial adaptations found in gracile Leporidae (rabbits and hares) and primitive features characteristic of extant Ochotonidae (pikas) and more robust leporids, suggesting that diversification within crown Lagomorpha and possibly divergence of leporids were already underway in the early Eocene (Rose *et al*., 2008). These leporid-like fossils are very similar to tarsal bones from the middle Eocene locality of Shanghuang in China and latest early Eocene of Andarak II in Kyrgyzstan (Averianov, 1991; Rose *et al*., 2008), and are more slender and more derived than the tarsals of *Dawsonolagus* from the late early Eocene Arshanto Formation of Inner Mongolia (Li *et al*., 2007). So, the lagomorphs of Vastan only suggest that leporid-like lagomorphs could originate already in the early early Eocene of India and disperse to Asia later.

The insectivore-like mammal *Indonyctia cambayensis* has been referred to the Holarctic family Nyctitheriidae, based on superficial resemblance to the asionyctiine *Voltaia* from the late Paleocene of Kazakhstan (Das *et al*., 2021). As we saw previously, *I. cambayensis* does not present the diagnostic characters of nyctitheres but well of cimolestans, a group of mammals present in the Paleocene and Eocene of Europe, Africa and India.

The perissodactyls *Vastanolophus* and *Cambaylophus* from Vastan are basal tapiromorphs with *Vastanolophus* sharing derived characters with helaletid tapiroids (Smith *et al*., 2015; Kapur & Bajpai, 2015; Bai *et al*., 2017). Because helaletids are known from Asia, they would represent one of the few links suggesting a direct migration between India and Asia. However, the oldest helaletids from Asia are not known before the late early Eocene and are contemporaneous with the earliest North American helaletids, suggesting that at least tapiroid perissodactyls originated in India (Smith *et al*., 2015). This paleobiogeographic scenario has become more complicated recently with the basal ceratomorph *Orientolophus* from the earliest Eocene Lingcha Formation in China forming a sister group with *Karagalax* from the early middle Eocene of Pakistan and *Cambaylophus* from the early early Eocene of India (Bai et al., 2018). Because another ceratomorph, *Gandheralophus* from the late early Eocene of Pakistan is part of another clade, Bai et al. (2018) proposed that ceratomorph perissodactyls dispersed twice to the Indian subcontinent during the early Eocene. This scenario does not include *Vastanolophus* and does not refute that only tapiroid ceratomorphs could originate already in the early early Eocene of India and disperse to Asia later. The presence of very basal perissodactylamorphans (=Perissodactyla + Antracobunia) such as cambaytheres in the early Eocene of India and Pakistan suggests that the origin of the different perissodactyl groups could be older than the earliest Eocene.

6.5. A TERMINAL COLLISION AFTER THE CONTINENTAL EARLY EOCENE GUJARAT FAUNAS

The present paleobiogeographic analysis of the continental vertebrate taxa from the Gujarat lignite mines of India indicates that most of them have European affinities; some are endemic to the Indian subcontinent; only a few have Gondwanan affinities; and none have direct Asian origin. This suggests that no terrestrial connection was yet established between India and Asia to allow terrestrial vertebrate exchanges in the early early Eocene, 54.5 Ma. An initial collision between the Indian subcontinent and Eurasia was maybe already existing at that time but no terminal collision. The analysis of the Vastan and Tadkeshwar vertebrate fauna is in agreement with a terminal collision occurring during the late early Eocene, ca. 50 My ago, in the west first (Zhuang et al. 2015; Yuan *et al.*, 2022) or quasi-synchronously closing of the Neotethys Ocean (Jin *et al.*, 2023).

7. Conclusions

Over 16 years of research (2004 to 2020) on early Eocene vertebrates from the Cambay Formation of Gujarat lignite mines, our Indian-American-Belgian team has published some 30 papers describing the Indian faunal assemblage. This assemblage originates from a unique freshwater to brackish paleoenvironment under tropical rain forest conditions around 54.5 My ago and presents several paleoecological specificities. The most relevant are that squamates are represented by a high diversity of acrodontan lizards (agamids) but no other contemporaneous lizard families. Snakes are very abundant and very diverse. Numerous mammals are arboreal such as the hyaenodontan, rodents, primates, bats and the apatemyid. Mammal predators are represented by a single hyaenodontan but no carnivoran is present. Mammal herbivores are represented by artiodactyls and perissodactylamorphans. Anthracobunians are numerous whereas basal tapiroids are rare and no other true perissodactyl family has been identified.

The paleobiogeographic specificities of Vastan and Tadkeshwar continental faunas indicate important affinities with Europe and not with Africa and Asia (=Laurasian taxa of European affinities) but a few relict taxa of Gondwanan affinities still persisted at that time among the non-mammalian vertebrates. This suggests that no terrestrial connection was yet established between India and Asia to allow terrestrial vertebrate exchanges at the early early Eocene, 54.5 Ma.

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Figure and table captions

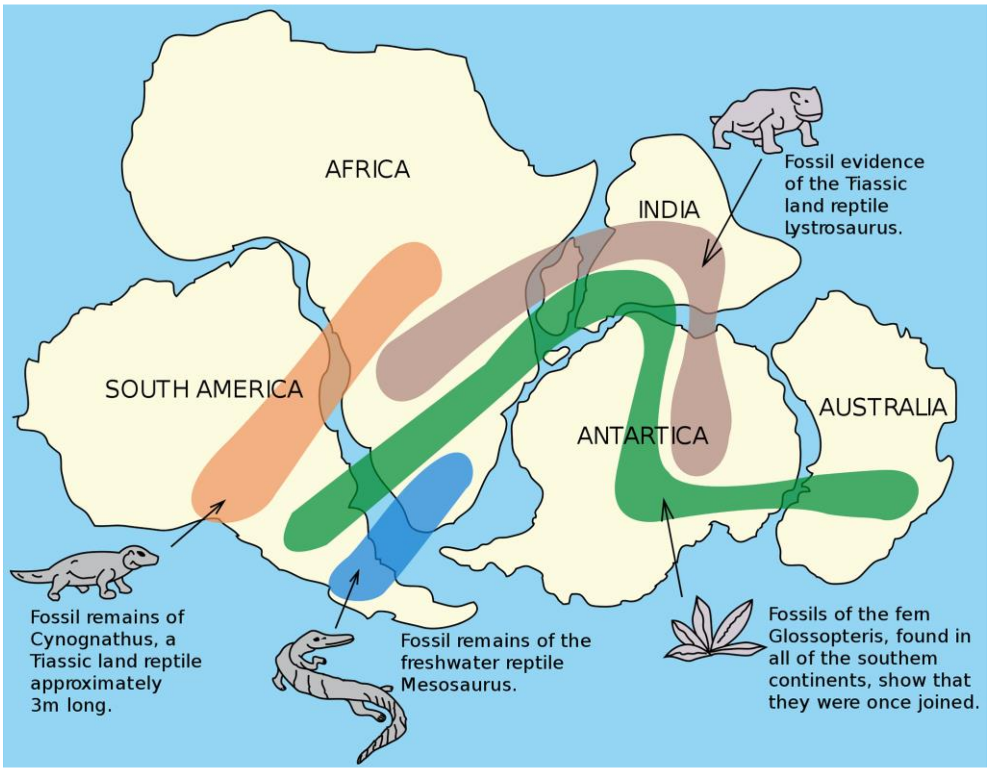

Fig. 1. – Schematic representation of the Gondwana landmass based on the concept of drifting continents by Wegener (1912), with India connected to other landmasses of the Southern Hemisphere based on common fossil terrestrial vertebrates and plants present today in the widely separated continents (Image in the public domain, originally from the United States Geological Survey).

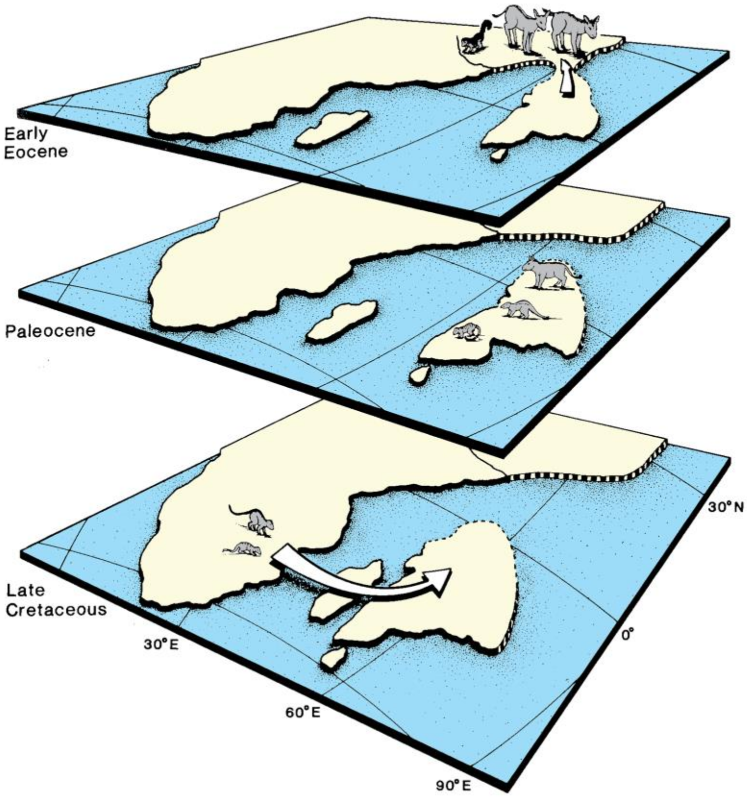

Fig. 2. – Schematic representation of hypothetical chronological events leading to the origin of several placental mammal higher taxa on the Indian subcontinent and their subsequent dispersal (from Krause & Maas 1990).

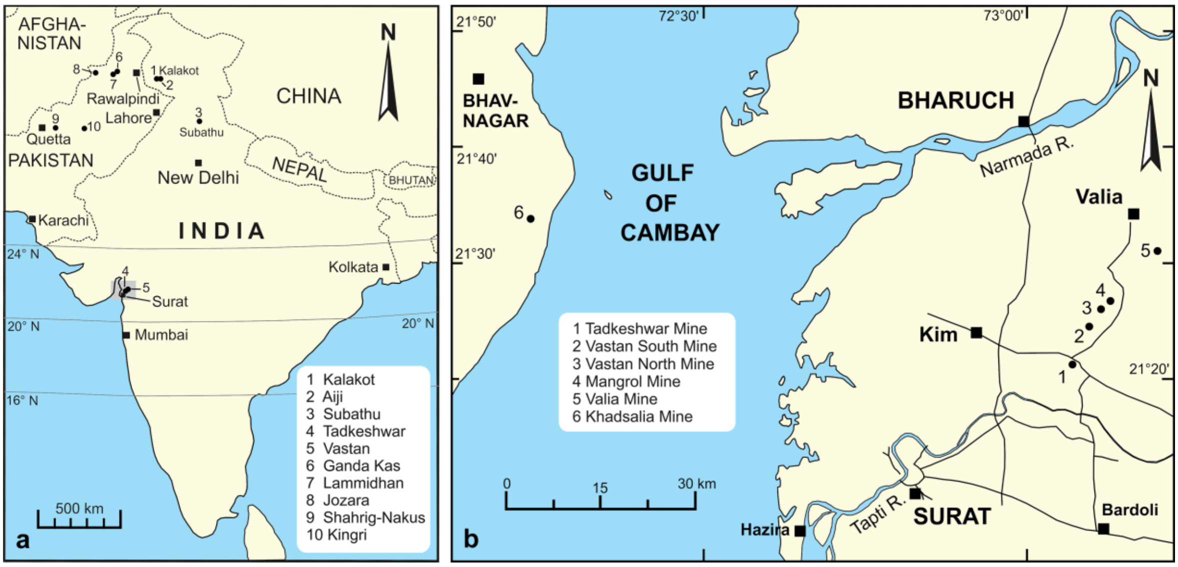

Fig. 3. – (a) Map of Indian subcontinent with location of early and middle Eocene terrestrial vertebrate localities in India and Pakistan. (b) Location map of the Gujarat lignite mines, including Vastan and Tadkeshwar mines, Surat district (from Rose et al. 2020).

Fig. 4. – (a) Vastan Lignite Mine on November 21st 2004. Dump trucks in front act as scales. (b) South-eastern part of Vastan South Lignite Mine on March 12th 2015. The early Eocene layers of the Cambay Formation (at left) overly the latest Cretaceous – earliest Paleocene Deccan Traps (at right). In between is a gap of about 10 million years. (c) Tadkeshwar Lignite Mine on March 7th 2020.

Fig. 5. – (a) Outcrop at Vastan Lignite mine after digging on November 17th 2004. The organic-rich lens of maximum 30 cm thick and about 5 m long just above the clay layer and below the lignite layer contained the first continental vertebrates. (b) Incisor of *Cambaytherium thewissi*, which was found at the contact between the lens and the clay layer (symbolized by an arrow on the outcrop in A). (c) R. S. Rana showing the maxillary with four teeth of *C. thewissi*. (d) Close-up on the maxillary with 4th decidual premolar and 1st and 2nd molars visible).

Fig. 6. – Surface collecting technique for large vertebrates by hand-picking after digging at Vastan mine in March 2011.

Fig. 7. – Screen washing technique for microvertebrates after breaking and drying the sediment; then melting in water and screen washing on meshes of 5 and 1 mm at Vastan mine in February 2006.

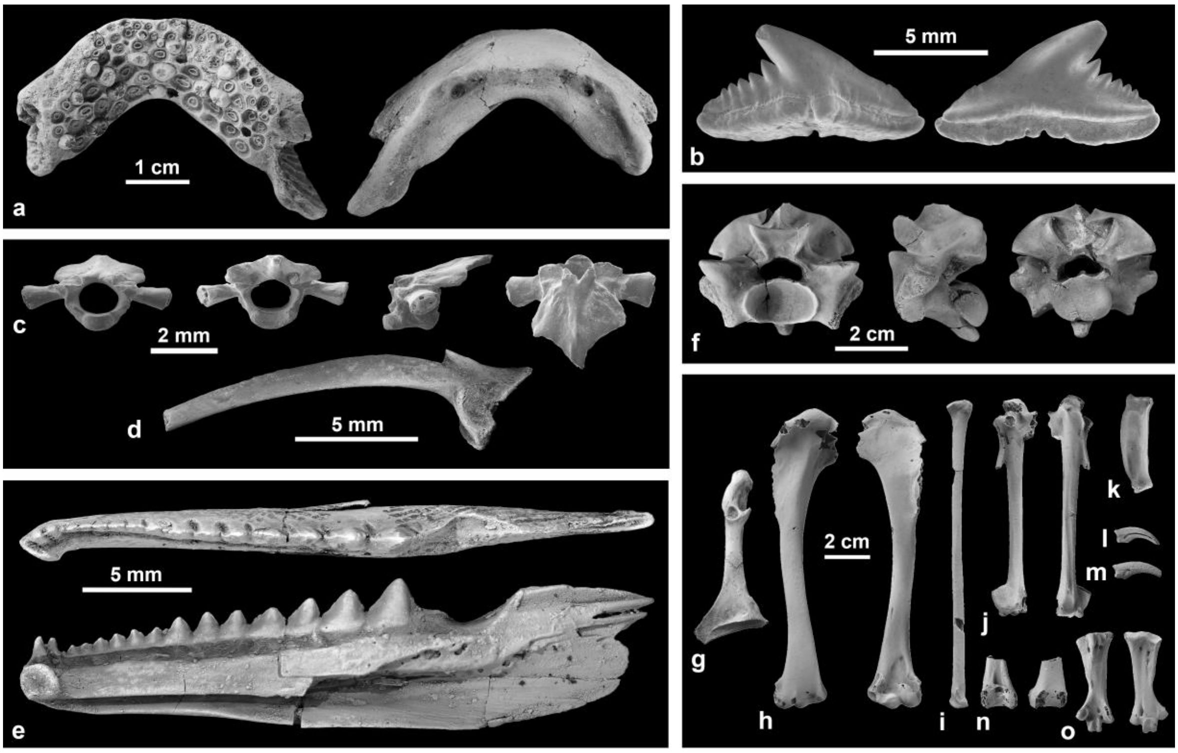

Fig. 8. – (a) Jaw of tetraodontiform fish *Avitoplectus molaris* (WIF/A 2340) in dorsal view and ventral views. (b) Upper antero-lateral tooth of the shark *Physogaleus* sp. (WIF/A 2339) in lingual and labial views. (c-d) Bombinatorid frog *Eobarbourula delfinoi*: (c) trunk vertebra (GU/RSR/VAS 5002) in anterior, posterior, lateral and dorsal views; (d) ilium (GU/RSR/VAS 5062) in lateral view. (e) Dentary of agamid lizard *Vastanagama susanae* (GU/RSR/VAS-2001) in occlusal and lingual views. (f) Anterior trunk vertebra of giant madtsoiid snake *Platyspondylophis tadkeshwarensis* (WIF/A 2269) in anterior, lateral and posterior views. (g-o) Psittaciform-like bird *Vastanavis*: (g) coracoid (GU/RSR/VAS 1802) in dorsal view; (h) humerus (GU/RSR/VAS 1802) in caudal and cranial views; (i) radius (GU/RSR/VAS 1688) in caudal view; (j) carpometacarpus (GU/RSR/VAS 1806) in dorsal and ventral views; (k) phalanx proximalis digiti majoris (GU/RSR/VAS 1807) in ventral view; (l-m) ungual phalanges (GU/RSR/VAS 1812-1813); (n) tibiotarsus distal end (GU/RSR/VAS 1808) in cranial and caudal views; (o) tarsometatarsus (GU/RSR/VAS 1809) in plantar and dorsal views.

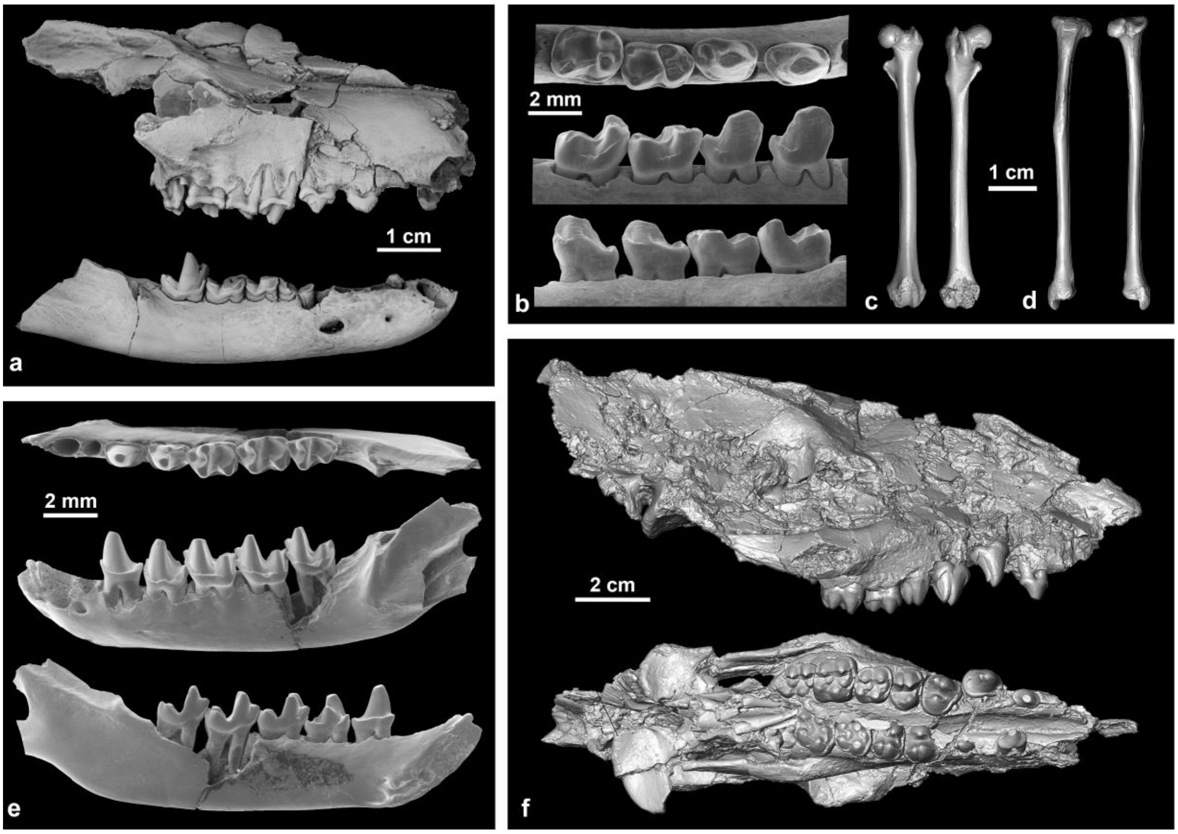

Fig. 9. – (a) Hyaenodontan carnivorous mammal *Indohyaenodon raoi*: skull (GU/RSR/VAS 1680) in lateral view and dentary (GU/RSR/VAS 767) in buccal view. (b-d) Adapoid primate *Asiadapis cambayensis*: (b) dentary (holotype GU/RSR/VAS 6); (c) femur (GU/RSR/VAS 756) and (d) tibia (GU/RSR/VAS 810) in anterior and posterior views. (e) Archaeonycterid bat *Protonycteris gunnelli* in occlusal, buccal and lingual views. (f) Anthracobunian *Cambaytherium thewissi*: skull (GU/RSR/VAS 402) in lateral and ventral (palatal) views.

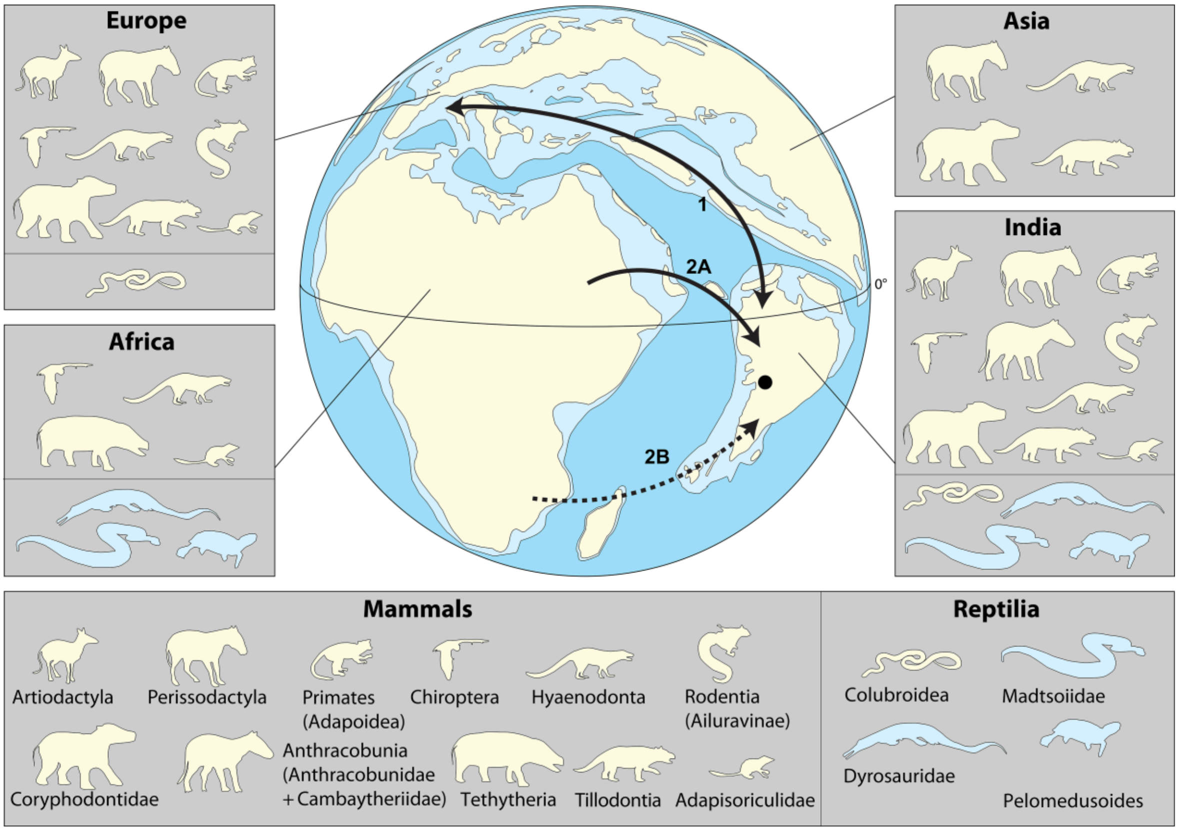

Fig. 10. – Paleogeographic reconstruction showing position of the Gujarat lignite mines (black dot) in the early Eocene, and possible dispersal routes of vertebrates around 54 My ago (adapted from Scotese, 2013). 1, Dispersal of taxa with European affinities between the Indian subcontinent and Europe across the Neotethys via the Kohistan-Ladakh island-arc system. 2A-B, Dispersal of taxa with Gondwanan affinities to the Indian subcontinent (2A) from Africa along the southern margins of the Neotethys or (2B) from Madagascar (ghost lineages originally dispersed during the late Cretaceous). Pale-blue animal outlines represent Gondwanan taxa and pale-yellow outlines represent Laurasian taxa.

Table 1

Continental vertebrates from the Cambay Formation in Gujarat. Occurrences in each mine and level are detailed in Rose *et al.* (2020).

Taxon	**Reference(s)**
CHONDRICHTHYES	
Carchariniformes	
Carcharhinidae	
Physogaleus sp.	Rana *et al.*, 2004; Smith *et al.*, 2016
Triakidae	
Galeorhinus sp.	Rana *et al.*, 2004; Rose *et al.*, 2006
Myliobatiformes	
Myliobatidae	
Myliobatis spp.	Rana *et al.*, 2004; Rose *et al.*, 2006; Smith *et al.*, 2016
Dasyatidae	
Dasyatis spp.	Rana *et al.*, 2004; Rose *et al.*, 2006
OSTEICHTHYES	

Amiiformes	
Amiidae indet.	Rose *et al*., 2006
Osteoglossiformes	
Osteoglossiformes indet.	Rana *et al*., 2004; Rose *et al*., 2006
Siluriformes	
Siluriformes indet.	Rose *et al*., 2006
Acanthopterygii	
Acanthopterygii indet.	Rose *et al*., 2006
Perciformes	
Sphyraena sp.	Rana *et al*., 2004; Rose *et al*., 2006
Eutrichiurides sp.	Rana *et al*., 2004; Rose *et al*., 2006
Tetraodontiformes	
Diodontidae	
Diodon sp.	Rana *et al*., 2004; Rose *et al*., 2006
Avitoplectidae	
Avitoplectus molaris	Smith *et al*., 2016; Bemis *et al*., 2017
AMPHIBIA	
Anura	
Bombinatoridae	
Eobarbourula delfinoi	Bajpai & Kapur 2008; Folie *et al*., 2013
Pelobatidae	
Eopelobates sp.	Folie *et al*., 2013
cf. *Eopelobates* sp.	Smith *et al*., 2016
« Ranidae »	
« Ranidae » indet.	Bajpai & Kapur 2008; Folie *et al*., 2013; Smith *et al*., 2016
Rhacophoridae	
Indorana prasadi	Folie *et al*., 2013
REPTILIA	
Testudinata	
Pleurodira	
Pelomedusoides indet.	Smith *et al*., 2016
Cryptodira	
Carettochelyidae indet.	Smith *et al*., 2016
Trionychidae indet.	Smith *et al*., 2016
Squamata	
Lacertilia	
Priscagamidae	
Heterodontogama borsukae	Rana *et al*., 2013
Agamidae	
Suratagama neeraae	Rana *et al*., 2013
Vastanagama susanae	Prasad & Bajpai, 2008; Rana *et al*., 2013
Indiagama gujarata	Rana *et al*., 2013
Tinosaurus indicus	Prasad & Bajpai 2008; Rana *et al*., 2013; Smith *et al*., 2016
Serpentes	
Madtsoiidae	
Madtsoiidae indet.	Rage *et al*., 2008; Smith *et al*., 2016
Platyspondylophis tadkeshwarensis	Smith *et al*., 2016
Boidae	
Boidae indet.	Rage *et al*., 2008; Smith *et al*., 2016
Palaeophiidae	
Palaeophis vastaniensis	Bajpai & Head 2007; Smith *et al*., 2016
Pterosphenus sp.	Rage *et al*., 2008
Russellophiidae	
Russellophis crassus	Rage *et al*., 2008
Russellophiidae indet.	Rage *et al*., 2008
Colubriformes	
Procerophis sahnii	Rage *et al*., 2008; Smith *et al*., 2016; Zaher *et al*., 2021
Thaumastophiidae	

Taumastophis missiaeni	Rage *et al*., 2008; Smith *et al*., 2016; Zaher *et al*., 2021
Caenophidia incertae sedis	
Gen. et sp. indet. A	Rage *et al*., 2008
Gen. et sp. indet. B	Rage *et al*., 2008
Crocodilia	
Crocodylomorpha	
Dyrosauridae	
cf. *Congosaurus* sp.	Smith *et al*., 2016
AVES	
Aves indet.	Mayr *et al*., 2010; Smith *et al*., 2016
?Psittaciformes	
Vastanavidae	
Vastanavis eocaena	Mayr *et al*., 2007
Vastanavis cambayensis	Mayr *et al*., 2010
Vastanavis sp.	Mayr *et al*., 2013; Smith *et al*., 2016
MAMMALIA	
Mammalia incertae sedis	
Pahelia mysteriosa	Zack *et al*., 2019
Adapisoriculidae	
Bharatlestes kalamensis	Kapur *et al*., 2017a, b
?Adapisoriculidae	
Indodelphis luoi	Bajpai *et al*., 2005a
Cimolesta	
?Palaeoryctidae	
Anthraryctes vastanensis	Bajpai *et al*., 2005b
?Cimolestidae	
Suratilestes gingerichi	Bajpai *et al*., 2005b
Indonyctia cambayensis	Das *et al*., 2021
Pantodonta	
cf. Coryphodontidae, indet.	Smith *et al*., 2016
Tillodontia	
Esthonychidae	
cf. *Esthonyx* sp.	Rose *et al*., 2009a
Anthraconyx hypsomylus	Rose *et al*., 2013
Indoesthonyx suratensis	Smith *et al*., 2016
cf. *Indoesthonyx suratensis*	Smith *et al*., 2016
Apatotheria	
Apatemyidae	
Frugivastodon cristatus	Bajpai *et al*., 2005b; Solé *et al*., 2020
Rodentia	
Ischyromyoidea	
Meldimys musak	Rana *et al*., 2008
cf. *Meldimys* sp.	Smith *et al*., 2016
?Ischyromyoidea	
Anthramys vastani	Bajpai *et al*., 2007
cf. Chapattimyidae	
Gen. et sp. indet.	Bajpai *et al*., 2007
Lagomorpha	
Lagomorpha indet.	Rose *et al*., 2008
Primates	
Asiadapidae	
Marcgodinotius indicus	Bajpai *et al*., 2005c; Rose *et al*., 2009b; Dunn *et al*. 2016; Smith *et al*., 2016
Marcgodinotius sp.	Rose *et al*., 2009b
Asiadapis cambayensis	Rose *et al*., 2007, 2009b; Dunn *et al*., 2016
Asiadapis tapiensis	Rose *et al*., 2018
cf. *Asiadapis* unnamed sp. nov.	Smith *et al*., 2016; Rose *et al*., 2018
Omomyidae	
Vastanomys gracilis	Bajpai *et al*., 2005c
Vastanomys major	Rose *et al*., 2009a; Dunn *et al*., 2016

Hyaenodonta	
Hyaenodontidae	
Indohyaenodon raoi	Bajpai *et al*., 2009; Rana *et al*., 2015; Smith *et al*., 2016
Insectivora	
?Erinaceomorpha	
Vastania sahnia	Bajpai *et al*., 2005b
Chiroptera	
Icaronycteridae	
Icaronycteris sigei	Smith *et al*., 2007
Archaeonycteridae	
Protonycteris gunnelli	Smith *et al*., 2007
Archaeonycteris? storchi	Smith *et al*., 2007
Palaeochiropterygidae	
Microchiropteryx folieae	Smith *et al*., 2007
Hassianycteridae	
Hassianycteris kumari	Smith *et al*., 2007
Cambaya complexus	Bajpai *et al*., 2005b; Smith *et al*., 2007
Family indeterminate	
Jaegeria cambayensis	Bajpai *et al*., 2005a; Smith *et al*., 2007
Undescribed larger bat	Smith *et al*., unpublished
“Eochiroptera” indet. 1	Smith *et al*., 2016
“Eochiroptera” indet. 2	Smith *et al*., 2016
Condylarthra?	
?Arctocyonidae	
?Arctocyonidae indet.	Bajpai *et al*., 2009
Anthracobunia	
Cambaytheriidae	
Cambaytherium thewissi	Bajpai *et al*., 2005b, 2006; Rose *et al*., 2006, 2014, 2020; Smith *et al*., 2016
Cambaytherium marinus	Bajpai *et al*., 2006; Rose *et al*., 2020
Cambaytherium gracilis	Smith *et al*., 2016; Rose *et al*., 2020
Perissodactyla	
Tapiroidea	
Vastanolophus holbrooki	Kapur & Bajpai, 2015
?Helaletidae	
Cambaylophus vastanensis	Smith *et al*., 2015
Artiodactyla	
Artiodactyla indet.	Kumar *et al*., 2010
Diacodexeidae	
Diacodexis indicus	Bajpai *et al*., 2005b; Kumar *et al*., 2010
Diacodexis parvus	Kumar *et al*., 2010
Diacodexeidae, indet.	Kumar *et al*., 2010