Dispersal vs. vicariance: the origin of India's extant tetrapod fauna

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Abstract

Given the Indian block's ancient association with Gondwana and subsequent separation from Africa, then Madagascar, then the Seychelles, vicariance has often been invoked to explain the distribution of some of India's extant biota that might have had Gondwanan origins. Here I review phylogenetic studies and fossil data of Indian tetrapods to ascertain the contribution of dispersal and vicariance in shaping the assemblage. Paleogene dispersal into India accounts for almost all of the tetrapod clades in India. Vicariance is invoked for three groups, all fossorial; the caecilians, the frog family Nasikabatrachidae and the blindsnake family Gerrhopilidae. This review concludes that practically all of India's Late Cretaceous tetrapod fauna (of Gondwanan origin) was extirpated during the Cretaceous-Paleogene mass extinction, which may have been exacerbated by the coeval volcanism associated with the emplacement of the Deccan Trap large igneous province. Subsequently, the tetrapod fauna was built up by incoming elements as India advanced towards Asia, docking with the continent in the Paleogene.

Highlights

- The role of plate tectonics-mediated vicariance in shaping the assemblage of Indian biota has been much debated in the last few decades.

- With the advent of molecular data, various biogeographical scenarios are been explicitly tested in a time-calibrated phylogenetic framework.

- Through review of global time-trees of various tetrapod groups from India I argue that much of the extant Indian tetrapod diversity dispersed into India post Gondwana break-up.

- For India fossorial soil invertebrates might be a better system than tetrapods to study plate tectonics-mediated vicariance.

Introduction

In the context of plate tectonics the Indian subcontinent is interesting given that most of this landmass was part of the Gondwana supercontinent through much of its geological history (Karanth 2006, Karanth 2015). The initiation of Gondwana breakup around 160 million years ago (Ma) and the resulting separation of the landmass constituting India and Madagascar (henceforth Indomadagascar) from Africa around 120 Ma was the earliest vicariance event experienced by Indian biota (Fig. 1a, 1b). This was followed by two later events, one due to India's separation from Madagascar around 90-85 Ma and another following the detachment of the Seychelles block around 65 Ma (Chatterjee and Scotese 1999, Briggs 2003, Ali and Aitchison 2008; Fig. 1c, 1d). Subsequently India advanced north across Indian Ocean, crossing the equator before colliding with Eurasia in the Eocene (some estimates have it at around 55 Ma, others 20 million years later; Briggs 2003, Aitchison et al. 2007,

Baxter et al. 2016; Fig. 1e, 1f). The accretion of India with Eurasia has been suggested to have facilitated faunal exchange between these landmasses (Mani 1974). This geological history of the Indian plate forms the basis for the out-of-India hypothesis or the Biotic Ferry model (See Datta-Roy and Karanth 2009 and references therein). According to this model, following separation from Madagascar, the rafting Indian plate carried faunal and floral elements from the Southern continents (presumably Gondwanan forms) to Asia. After docking with Asia these lineages then disperse out of India. Thus, it has been postulated that the Indian biota today comprises a mixture of older Gondwanan forms plus younger elements that crossed over into India from Africa and Asia (Mani 1974). In this work, I refer to those lineages that have existed in India since before the initial breakup of Gondwana in the Early or Middle Jurassic as "Gondwanan forms" (c. 170 Ma).

Fossil records from India lend some support to India's biotic history described above. The Upper Cretaceous assemblages include numerous taxa with
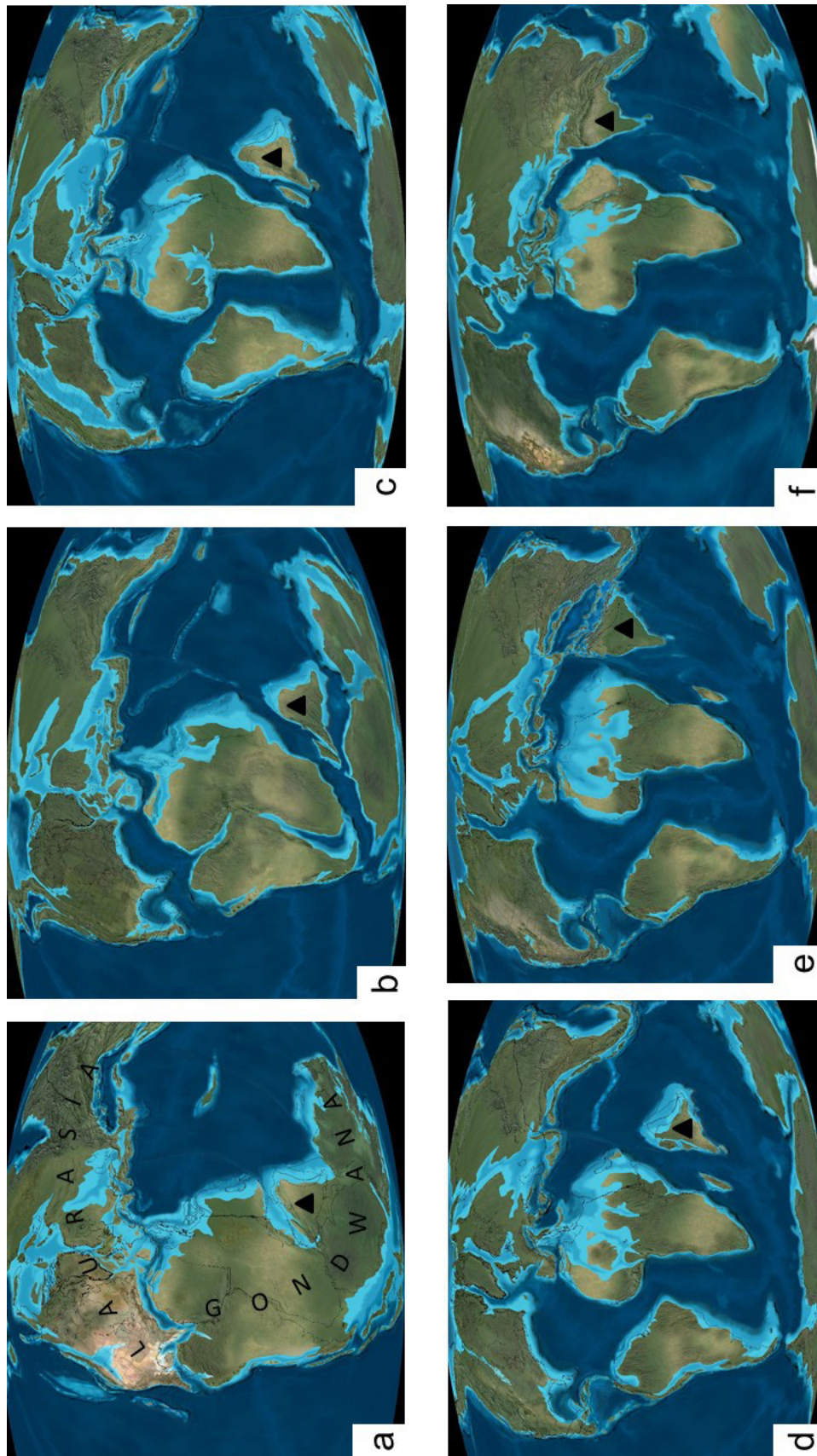
Figure 1. The position of Indian plate (black triangle) from 170 to 35 Ma; a) India part of Gondwana around 170 Ma, b) Indomadagascar separates from Africa 120 Ma, c) India and Madagascar separate from each other around 85 Ma, d) India's position at 65 Ma when Seychelles separates from India, e) India's initial contact with Eurasia 55 Ma, f) India's final collision with Eurasia 35 Ma. Image credit: © 2016 Colorado Plateau Geosystems Inc.

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Gondwanan affinities, including leptodactylid, hylid and ranoid frogs, madtsoiid and nigerophiid snakes, pelomedusoid turtles, mesosuchian crocodiles, abelisaurid dinosaurs, and gondwanathere mammals (Prasad and Sahni 2009). In contrast, the Lower Eocene comprises mainly forms with Eurasian affinities such as pelobatid frogs, russellophiid snakes, parrot-like birds, bats, rodents, adapoid primates, artiodactyls, etc (Smith et al. 2016). Given this scenario, India provides an interesting setting for studying the relative contributions of dispersal and vicariance in shaping the biotic composition of this region.

In this regard, molecular data are being increasingly used to address this question (Karanth 2006, Datta-Roy and Karanth 2009, Joshi and Karanth 2011, Krosch et al. 2012, Toussaint et al. 2016, Sil et al. 2020). However, for a robust test of these two contrasting hypotheses it is imperative to reconstruct time-calibrated evolutionary trees of taxa sampled from multiple Gondwanan fragments, particularly Africa, Madagascar and India (Datta-Roy and Karanth 2009). The vicariance scenario would be supported when higher level relationships and the divergence of the corresponding nodes mirror the sequence and timing of plate separation, i.e., separation of African from Indo-Malagasy forms around 120 Ma followed by separation between Malagasy and India taxa around

90-85 Ma (See fig. 2). Alternatively, if the ingroup under consideration underwent diversification relatively recently (after 85 Ma to present) then, irrespective of the topology, vicariance can be rejected. This is because in such cases the origin of the group as a whole would be too recent for Gondwana vicariance to have played any role in their distribution. For example, the cichlid fishes that occur in all the former Gondwana fragments (except Australia) provide an interesting system to study the role of dispersal vs. vicariance in shaping their pantropical disjunction. The cichlid phylogeny is congruent with the sequence of plate separation in that the African forms are sister to a clade consisting of Indo-Malagasy forms. However, molecular dating suggests that the divergence among these lineages occurred long after plate separation (Vences et al. 2001, Crottini et al. 2012). Thus, in the case of the cichlids, dispersal better explains their current distribution. Clearly, invoking vicariance based primarily on Gondwanan distribution and tree topology can be problematic. A crucial component in such studies is the integration of temporal information in dispersal-vicariance analysis (Donoghue and Moore 2003). Since the synthesis by Datta-Roy and Karanth (2009), many global phylogenies of various groups have been published, thus providing an opportunity to revisit this issue.
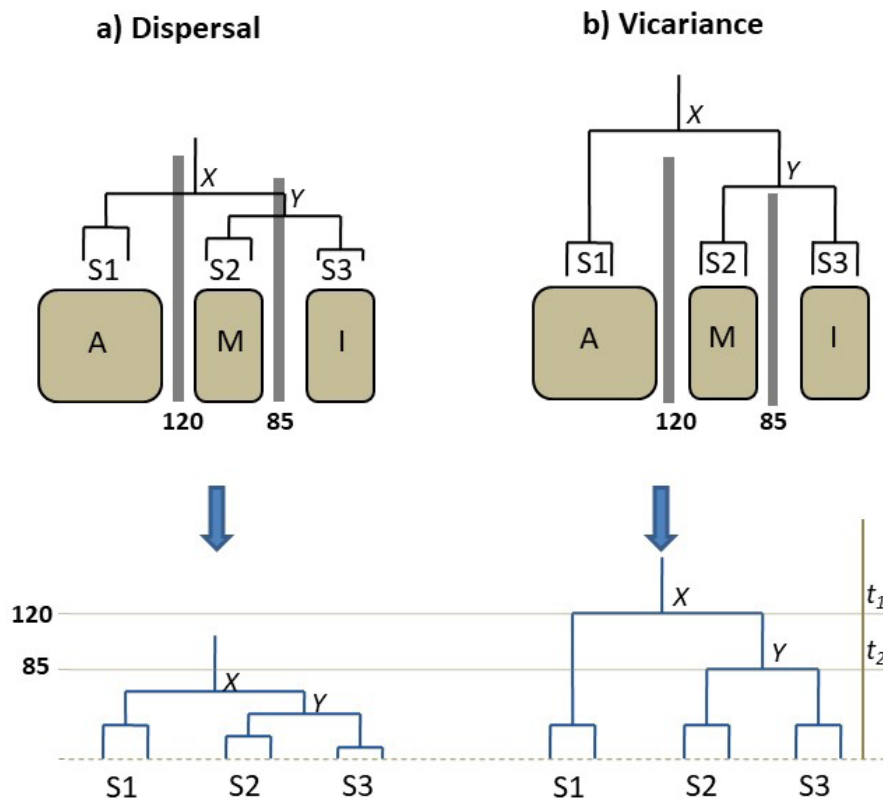

Figure 2. Hypothetical phylogenetics trees depicting dispersal (a) and vicariance (b) to explain the distributions of taxa S1, S2 and S3 in Africa (A), Madagascar (M) and India (I) respectively. Under the dispersal scenario the taxonomic group (crown group representing S1, S2, S3) undergoes diversification after the emergence of barriers. Here the dates corresponding to the internal nodes X and Y postdate the separation of Africa-Indomadagascar (t_1=120 Ma) and India-Madagascar (t_2=85 Ma). Whereas in case of the vicariance scenario inferred dates for X and Y overlap with t_1 and t_2.

India here refers to the Indian subregion, which has been assigned to a separate biogeographical unit by various authors (Wallace 1876, Blanford 1901, Mani 1974, Corbet and Hill 1992, Bansal and Karanth 2010, Sil et al. 2020) to highlight its unique biota and evolutionary history (Fig. 3). It constitutes the region south of the Himalayas, including peninsular and central India, and Sri Lanka, but excludes the Indus and Gangetic plains as well as the Thar desert that were formed recently after India's accretion to Asia. However, the northern boundaries of this subregion vary across these classifications. The islands of Lakshadweep, and Andaman and Nicobar archipelagos are also excluded. Lakshadweep islands are of recent oceanic origin, whereas the Andamans and the Nicobars fall in the Indo-Chinese and Sundaic subregions, respectively.

Recent global time-trees of a range of tetrapods are reviewed here to better understand the relative contributions of dispersal and vicariance, in the context of plate tectonics, in shaping the biotic composition of India. The tetrapod groups included are amphibians (anurans, caecilians and salamanders), mammals, squamates (snakes and lizards), testudines, crocodilians and birds. These global phylogenies are at different levels of taxonomic hierarchy: birds and mammals are at the order level; squamates and anurans at the family level, caecilians and testudines at the generic level, and crocodilians at the species level. For each of these global phylogenies the representation from

India was 100% for the corresponding taxonomic hierarchy; for example, all the orders of Indian birds were represented in the global bird phylogeny. Taxa whose crown group age predated the separation of Africa and Indomadagascar (160–120 Ma) and / or India and Madagascar (90–85 Ma) were considered as a strong candidate for vicariance. Those that underwent diversification after 85 Ma were categorised as elements that dispersed into India (Fig. 2). Drawing upon a mixture of molecular phylogenetic studies and palaeotological reports I provide a comprehensive overview of the origins and assembly of the Indian tetrapod assemblage.

Origins of Indian tetrapods

Amphibians

The crown group age of major amphibian clades, anurans, caecilians and salamanders, fall in the Triassic (250-200 Ma; Roelants et al. 2007), which predates Gondwana breakup. Thus, given their antiquity and lack of tolerance to salt water, amphibians have long been considered a poster group for testing plate tectonic mediated vicariance (Bocxlaer et al. 2006).

Anurans

Based on molecular dating of ranid frogs, Bossuyt and Milinkovitch (2001) invoked vicariance to explain
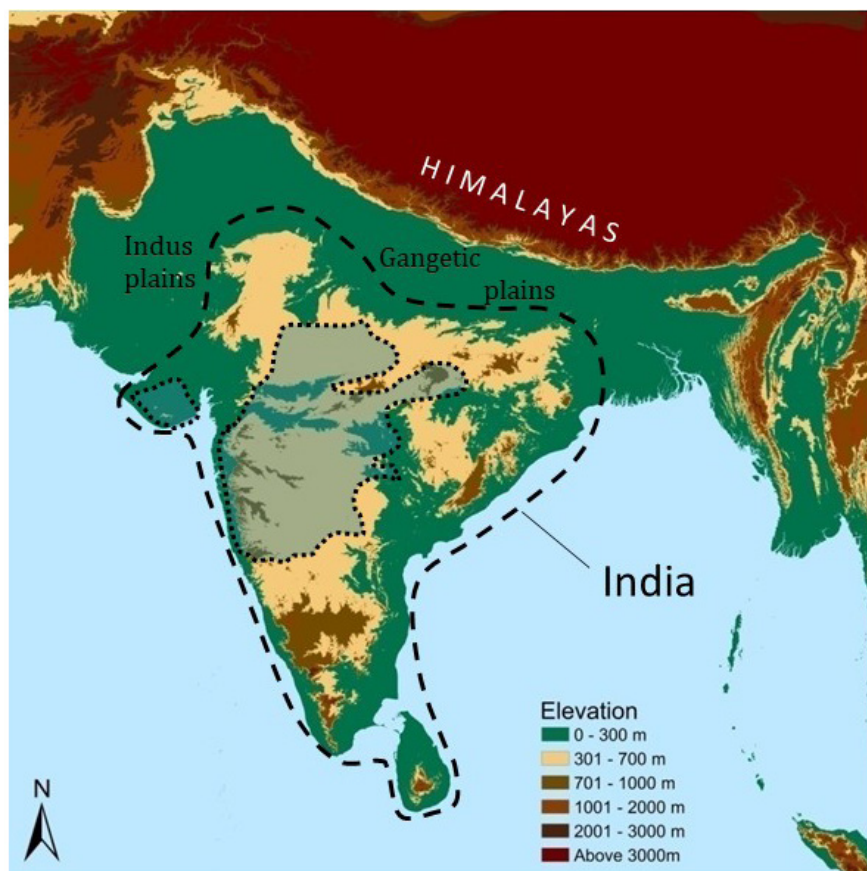

Figure 3. Physiographical map of southern Asia. The dash line represents the borders of the Indian subregion (see text for details). The extent of Deccan Traps is depicted by dotted line. Modified from Karanth 2015.

the distribution of certain frog families such as Mantellidae and Rhacophoridae in Madagascar and India respectively. Their study suggested an out-of-India dispersal of many ranid lineages. Bossuyt et al. (2006) undertook a wider sampling and opined that Eurasia colonization of ranids from Africa was also plausible. Bocxlaer et al. (2006) concluded that current distribution of major Old World frog lineages can be better explained by Late Cretaceous dispersal via the terrestrial connections between most adjacent Gondwanan landmasses. Thus, the latter two studies question the out-of-India scenario that was initially proposed to explain the distribution of Asian anurans. It should be noted, however, that these studies lacked a comprehensive sampling of anuran families from the Old World and were limited in terms of number of markers and fossil calibrations. In this regard, the recent paper by Feng et al. (2017) is of much interest, as it included 44 of the 55 global frog families and, importantly, all of those found in India. Their age-calibrated phylogeny based on 20 fossil calibrations suggests that most of the frog families that are endemic to India, and those distributed in Eurasia, diverged from their African and Malagasy counterparts around the Cretaceous–Paleogene (K-Pg) boundary (66 Ma). Thus, these events occurred appreciably later than the separation of Africa and Indomadagascar, and India and Madagascar. Furthermore, their biogeographical analyses indicate that eight out of the nine anuran families that are present in India have dispersed from Eurasia in the Cenozoic. The one exception is the endemic family Nasikabatrachidae, which is sister to Sooglossidae from Seychelles (Feng et al., 2017). The granitic islands of the Seychelles sit above a Gondwanan fragment that separated from peninsular India around 65 Ma and the divergence date for these two families is consistent with this geological date. Additionally, the divergence of Nasikabatrachidae-Sooglossidae lineage from the ranoid frogs of the Old World fits with the geological time for the separation between Indomadagascar and Africa. The Upper Cretaceous anuran fossils of India are represented by groups that are currently not found in India, including Discoglossidae, Hylidae, Pelobatidae and Myobatrachidae (Khajuria and Prasad 1998, Khosla and Sahni 2003). Lower Eocene anuran fossils from Vastan mines in Gujarat, western India consists of Bombinatoridae (super family Discoglossoidea), Pelobatidae, Rhacophoridae and Ranidae (Folie et al. 2013), but only the last two are currently found on the sub-continent. This turnover suggests a gradual replacement of Cretaceous anuran fauna by intrusive elements in the Cenozoic.

Caecilians

Caecilians have also been invoked as an exemplar of the out-of-India scenario given their antiquity and circumtropical distribution (see Wilkinson et al. 2002, Gower et al. 2002). Caecilians are found on all of the former Gondwanan fragments except Madagascar and Australia. The three Asian caecilian families, Indotyphlidae, Chikilidae and Ichthyophiidae, diverged from their West Gondwanan counterparts over 120 Ma

(Kamei et al. 2012). Thus, these dates suggest their Gondwanan history and the role of Indomadagascar-Africa vicariance in shaping their distribution. However, it must be noted that molecular dating analysis in these studies have been based on a mitochondrial dataset (Wilkinson et al. 2002) or a combined mitochondrial and nuclear dataset in which the mitochondrial markers dominated the dataset (Kamei et al. 2012). These dates need to be revalidated using a "nuclear only" dataset as there is often incongruence between mitochondrial and nuclear markers with respect to tree topology as well as divergence date (see Jana and Karanth 2019, and the references therein). Additionally, the absence of caecilians from Madagascar is intriguing. It is plausible that they went extinct in Madagascar. However, it is also possible that the dates have been over estimated and caecilians dispersed onto the drifting Indian plate from Africa (as suggested by Briggs 2003). There is an increasing body of molecular data supporting such direct dispersal of amphibians and reptiles onto the drifting Indian plate from Africa/Asia presumably via land bridge (Bocxlaer et al. 2006, Bansal and Karanth 2013). It should be noted that no caecilian fossils have been reported from India.

Salamanders

Salamanders in Asia have a largely Palearctic distribution; the two species from India are from the Eastern Himalayas. This region falls outside of the Indian subregion and therefore not relevant here. Moreover, work by Zhang et al. (2008) suggest that the Asian salamandrids dispersed to eastern Asia from Europe around 29 Ma.

Mammals

Currently, only placental mammals are present in India. Three recent studies that reconstructed the global time-calibrated phylogeny of placental mammals are relevant. Tarver et al. (2016) suggest that the diversification of the placental orders took place 76–51 Ma; similarly, Liu et al. (2017) estimates fall between 75 and 55 Ma and thus straddles the K-Pg mass extinction. Upham et al. (2019) report that most of the divergence events among placental mammals have confidence limits that overlap the K-Pg. The critical issue, therefore, is that the event post-dates the India-Madagascar vicariance. Thus, the presence of some of these orders in India must have resulted from incoming dispersals. Clyde et al. (2003) stated that during the initial collision, modern orders of mammals dispersed into India rather than out of it. In this regard, Tarver et al. (2016) stated that their results are compatible with placental diversification being driven by dispersal rather than vicariance. This idea is supported by the Indian paleontological record, which exhibits high diversity of placental mammals in the Early Eocene, during India's initial collision with Eurasia (Smith et al. 2016, Chatterjee et al. 2017).

Birds

As with mammals, the bird record also supports rapid diversification around the K-Pg transition

(Jarvis et al. 2014, Claramunt and Cracraft 2015, Prum et al. 2015, Kimball et al. 2019). In these studies the root node of neoaves falls in the Late Cretaceous, 75-65 Ma. Furthermore, these studies also support a Late Cretaceous divergence between landfowls (Galliformes) and waterfowls (Anseriformes). Thus, inter-ordinal diversification among birds (excluding ratites) occurred after India-Madagascar separation. Fossil data lends additional support to this scenario. According to Feduccia (2003) even though birds evolved in the Late Jurassic (around 157 Ma) and underwent diversification through much of Cretaceous, these lineages were badly depleted during the K-Pg event and only a few morphological forms survived to evolve into the extant lineages we see today. Longrich et al. (2011) noted that there was a major extinction of archaic birds coinciding with the K–Pg boundary. Similarly, Brusatte et al. (2015), based on fossil data, concluded that most avian lineages were decimated at the end-Cretaceous extinction, alongside their close dinosaurian relatives and after this mass extinction modern birds emerged.

Crocodilia

The crocodilian genus *Crocodylus* is often referred to as an ancient morphologically conserved group whose circumtropical distribution was shaped by continental drift (see Oaks 2011 and reference therein). India harbours three crocodilian species, *Crocodylus palustris* and *Crocodylus porosus* (family Crocodylidae), and *Gavialis gangeticus* (family Gavialidae). The third crocodilian family, Alligatoridae, has been reported from Upper Cretaceous beds in India (Khosla and Sahni 2003). Oaks (2011) suggests that the all modern crocodilians date back to the Late Cretaceous. More importantly the diversification of Afro-Asian crocodilians began around the Paleocene-Eocene boundary (around 56 Ma), well after India and Madagascar had separated. Thus, the three species of crocodilians that are present on India dispersed to the landmass.

Squamates

The squamate reptiles represented consist of over 9700 species and are thus one of the most species-rich tetrapod groups (only the birds have comparable numbers, around 10000 species). Most molecular studies support a Late Jurassic to Early Cretaceous origin of all the major clades of squamates (see Zheng and Wiens, 2016 and the references therein). These age estimates fall within the range of the three vicariant events discussed earlier. India harbours seven families of lizards including Eublepharidae and Gekkonidae (geckos), Scincidae (skinks), Lacertidae (lacertids), Agamidae (Agamids), Varanidae (monitor lizard), Chamaeleonidae, (chameleons) and multiples families of Serpentes (snakes).

Geckos

Most of India's gecko diversity (seven out of eight genera) is in the family Gekkonidae. The age of the root node of Gekkonidae varies depending on the study from 65 Ma (Burbrink et al. 2020) to 85 Ma (Gamble et al. 2011). These dates fall outside the age of Africa-Indomadagascar plate separation but are within the period of India-Madagascar separation. India and Madagascar share two Gekkonid genera, *Hemidactylus* and *Phelsuma*. *Hemidactylus* species in Madagascar are mostly human commensals that have probably been introduced as they exhibit very little variation (Vences et al. 2004). *Phelsuma* is related to Southwest African genera *Rhoptropella* (Austin et al. 2004) and *Lygodactylus* (Pyron et al. 2013). Importantly, phylogenetic and biogeographical studies undertaken thus far suggest that most Gekkonid genera in India dispersed into India well after the India-Madagascar separation. These include *Dravidogecko* that dispersed to India around 70 Ma (Bansal and Karanth 2013) and *Hemidactylus* around 35 Ma (Bansal and Karanth 2010) from Eurasia/ Africa, *Cyrtopodion* (Agarwal et al. 2014) from the Middle East around 10 Ma, *Cyrtodactylus* (subgenus *Geckoella*) (Agarwal and Karanth 2015) and *Hemiphyllodactylus* (Agarwal et al. 2019) from Southeast Asia around 35 Ma. Thus, Malagasy and Indian Gekkonids have disparate evolutionary histories.

The family Eublepharidae has a Laurasian origin that dispersed into Africa in the Early Miocene after these landmasses connected (Jonniaux and Kumazawa 2008). Thus, its presence in India can only be explained by dispersal post India-Eurasia collision. The oldest gecko fossil in the world is *Cretaceogekko* from the Lower Cretaceous, 97–110 million year (my) old amber from Myanmar (Arnold and Poinar 2008). However, so far, no gecko fossils have been recovered in Indian deposits, lending support to the idea that geckos dispersed into India recently.

Chameleons

Chameleons are distributed in Africa, Madagascar, Seychelles (among other islands in Arabian sea) and India making them an ideal group to test the Gondwana vicariance hypothesis. However, molecular studies have conclusively demonstrated a post Gondwana break-up dispersal of chameleons into India, either through transoceanic dispersal from Africa or geodispersal from Africa via Arabia (Raxworthy et al. 2002, Tolley et al. 2013).

Skinks

According to the recent squamate time-trees the Scincidae crown group began diversifying around 100 Ma (Zheng and Wiens 2016, Simões et al. 2018). Thus, the separation of Africa and Indomadagascar is unlikely to have shaped their distributions. India and Madagascar harbour two scincid subfamilies, namely Lygosominae and Scincinae. Honda et al. (2003) undertook global phylogenetic analysis of lygosomines that included most of the widely distributed genera (including *Mabuya*). In their phylogeny, Malagasy *Mabuya* was nested within a larger Africa clade. Work done by Karin et al. (2016) suggested an out-of-Asia diversification of the circumtropical '*Mabuya*' group in the Eocene. Thus, Malagasy lygosomines have an Asian origin and reached Madagascar recently, via Africa. In the global phylogeny of squamates by

Pyron et al. (2013), the Scincines cluster into two groups, one consisting of Laurasian forms and the other representing Afro-malagasy lineages. Work undertaken by Whiting et al. (2004) suggest that Malagasy Scincine are related to African forms and appear to have reached Madagascar by dispersal over water, rather than as a result of vicariance. However, in these studies Indian species were not included, thus phylogenetic position of Indian Scincines remains unresolved. Thus, Indian lineages could have dispersed from Laurasia, Africa or Madagascar.

Lacertids

Among the multiple genera of lacertids found in South Asia, only *Ophisops* is found in India. Agarwal and Ramakrishnan (2017) undertook a time-calibrated biogeographical analysis of this group. They suggest that *Ophisops* dispersed into India from the Saharo-Arabian Realm in the Oligocene.

Agamids

Much of agamid diversity of India is in the subfamily Draconinae, whereas subfamily Agaminae is largely distributed in the fringe areas of India and beyond. Macey et al. (2000) speculated that the Draconinae clade in Asia might be of Indian (out-of-India) or Southeast Asian (into India) origin. However, phylogenetic and biogeographic analyses undertaken by Grismer et al. (2016) suggest that multiple lineages of Draconinae dispersed into India from Eurasia during the Eocene. In agreement with molecular results agamids have been reported from early Eocene fossil deposits in Vastan, India (Rage et al. 2008).

Monitor lizards

The family Varanidae represented by genus the *Varanus* is distributed in Asia, Africa and Australia. Vidal et al. (2012) suggest an Asian origin of Varanidae followed by a dispersal into Africa and Australia in the Late Eocene.

Snakes

Snakes in India are represented by both the major clades of Serpentes, i.e., Alethinophidia (advanced snakes) and Scolecophidia (blindsnakes). Recent molecular studies infer a range of ages for the crown group Alethinophidia: 82 Ma (Miralles et al. 2018), 92 Ma (Zheng and Wiens 2016) and ~100 Ma (Hsiang et al. 2015, Harrington and Reeder 2017). These dates fall within the time frame of India-Madagascar separation. The earliest split within Alethinophidia, between Amerophidia and Afrophidia, corresponds to South America-Africa separation (Vidal et al. 2007). However, all families in Afrophidia arose post K-Pg mass extinction in the Paleogene (Burbrink et al. 2020). Among the two families of advanced snakes of Madagascar, colubrid lineages are nested within multiple clades of African colubrids (Lawson 2005, Vences 2004); similarly, Malagasy members of Boidae are sister to African species (Noonan and Chippindale 2006a, Reynolds et al. 2014). Given Indian and Malagasy forms are not sisters (not immediate ones, at least),

and these families arose in the Paleogene, vicariance due to India-Madagascar separation can be ruled out as a possible mechanism for their current distribution. Interestingly both Colubridae and Boidae appear in the Early Eocene fossil deposits in Vastan, India (Rage et al. 2008). The authors also note an overall similarity of Vastan fauna to that of the Early Eocene of Europe. Additionally, the Early Eocene also represent a time when the Indian plate was close to Eurasia, therefore presence of these lineages in India is better explained by dispersal.

Scolecophidians constitute an ancient group of burrowing snakes that are distributed in all the Gondwanan fragments (South America, Africa, Madagascar, India and Australia; Vidal et al. 2010). The crown group scolecophidians began diversifying in the Early Cretaceous (Miralles et al. 2018) around the time when the Gondwana breakup was initiated. The phylogenetic and biogeographical study undertaken by Vidal et al. (2010) suggest a Gondwanan origin of blindsnakes with the earliest diversification overlapping with a vicariant event: the separation of Africa and Indomadagascar around 150 Ma. This was followed by another vicariance event that corresponds to India-Madagascar separation. The blindsnake lineage that became isolated on the Indian plate (family Gerrhopilidae) was carried by the rafting Indian plate to Asia (out-of-India). Among squamates, scolecophidians are perhaps the only example of a group with a Gondwanan history whose distribution has been shaped by multiple vicariance events. Unfortunately, there are no records of scolecophidian fossils from India to fortify this conclusion.

Overall, the molecular studies reviewed above suggest that Indian squamate diversity was derived from Africa and Asia. Many of these dispersal events occurred after India's collision with Asia. The only Gondwanan lineage surviving in India are the blindsnakes of the family Gerrhopilidae. Thus, it appears that most of India's squamate diversity with Gondwanan history went extinct. Incidentally, squamate fossil data from North America exhibit 83% decline in species diversity and a dramatic decline in morphological diversity across the K-Pg (Longrich et al. 2012).

Testudines

Vicariance has been invoked to explain the distribution of freshwater turtles of the family Podocnemidae in South America and Madagascar (Noonan and Chippindale 2006b). However, this family is not present in India nor is there an associated fossil record. Global phylogenetic and biogeographical analyses of Testudines undertaken by Pereira et al. (2017) suggest that India's tortoise and freshwater turtles are the result of multiple dispersal events from Southeast Asia from the Eocene to the Miocene.

Discussion

India's unique geological history has motivated biogeographers to propose that its biota is composed of both ancient Gondwanan elements and more recent

arrivals from Asia and Africa. A Gondwanan history for a given lineage would suggest that its distribution in the former Gondwanan fragments has been shaped by vicariance. However, the molecular data suggests that much of the tetrapod diversity of India is the result of post K-Pg mass extinction colonization (Fig. 4). There are three exceptions to this pattern: the caecilians, frog family Nasikabatrachidae and the blindsnake family Gerrhopilidae. The out-of-India hypothesis is supported by certain caecilian and blindsnake lineages, whereas the nasikabatrachids are a Gondwanan relict. Remarkably, the earliest fossil evidence of modern frogs, agamids, and placental mammals appear abruptly in India during the Early Eocene (Chatterjee et al. 2017), long after the K-Pg mass extinction. Thus, the molecular studies and limited fossil data suggest that dispersal better explains the distributions of modern tetrapod taxa of India. Furthermore, given the root ages of the extant tetrapod groups, vicariance can be ruled out as the possible reason for their current distributions in other Gondwanan fragments such as Madagascar and Australia. In this regard, studies have pointed out that the extant Malagasy vertebrate fauna was largely assembled through dispersal from Africa post separation (Yoder and Nowak 2006, Crottini et al. 2012).

However, the above conclusion is not consistent with Late Cretaceous fossils from India that are of largely Gondwanan origin. It is plausible that the K-Pg mass extinction might have obliterated some of India's Gondwanan biota. Globally, dinosaurs, pterosaurs, marine reptiles and two-thirds of all marine life became extinct

with the termination of the Cretaceous Period (Feduccia 2003). Squamates and birds also experienced similarly large depletions (Longrich et al. 2011, Longrich et al. 2012). In the case of Indian fauna two additional factors might have compounded extinction. Much of India's Gondwanan biota might have been under great climatic stress due to the rapid northward drift of the sub-continent at the time (Raven and Axelrod 1974, Mani 1974). Moreover, there was major volcanism associated with the Deccan Traps (Fig. 3) that took place in the Late Cretaceous-Early Palaeocene (Thewissen and McKenna 1992, Renne et al. 2015, Schoene et al. 2015, Sprain et al. 2019). At the beginning of the Paleogene, the Indian plate had probably lost much of the tetrapod diversity it had in the Cretaceous. Thus, as India moved northward from Gondwana to Eurasia, the faunal composition changed from Gondwanan affinity to Asian affinity as new forms washed in and later walked over (Chatterjee et al. 2017).

Does this mean that India does not harbour any animal lineages with Gondwanan history? Perhaps the right taxa are not being targeted. Notably, the three tetrapod groups of Gondwanan history discussed here are all fossorial. It has been noted that stable and predictable fossorial environments shelter species from dramatic above-ground environmental changes (see Cyriac and Kodandaramaiah 2018 and the references therein). In this regard, soil invertebrates might be a promising group to address this question. Given that soil invertebrates tend to be small and fossorial they are more likely to be shielded from extreme conditions
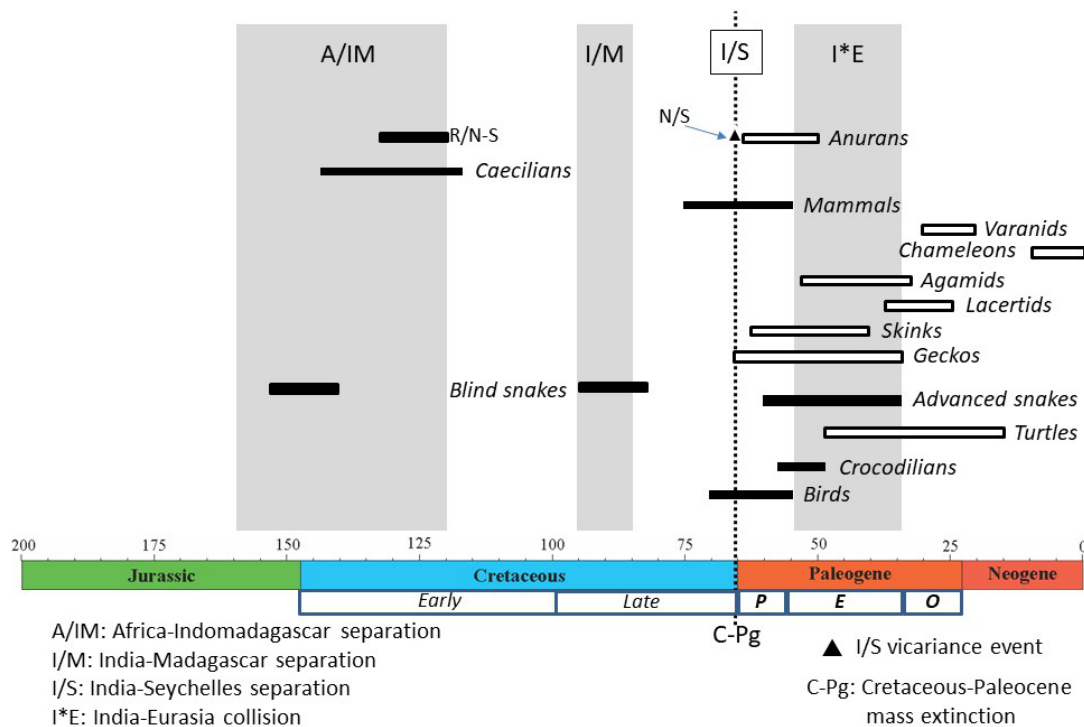

Figure 4. Summary of the origin of Indian tetrapods. Solid black bars represent the range of dates for basal diversifications in the respective groups. Open bars depict the range of dates for dispersal into India for various extant taxa based on biogeographical analyses. R/N-S: divergence of ranoid frogs from the Nasikabatrachidae-Sooglossidae lineage. N/S: divergence between Nasikabatrachidae and Sooglossidae from India and Seychelles respectively. P: Paleocene; E: Eocene; O: Oligocene.

on the surface. One such group are the centipedes, where studies have reported multiple lineages with Gondwanan history (Joshi and Karanth 2011). Overall, the bulk of the India's tetrapod diversity results from Cenozoic immigration. It would be interesting to determine if these dispersal events were transoceanic or geodispersal. Lineages that descended from the initial passengers that were present back in the Cretaceous probably had unusual life modes that enabled them to survive the K-Pg extinction event, Deccan Trap volcanism and challenging environmental shifts associated with India's rapid migration through the climatic belts.

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References

Agarwal, I., Bauer, A.M., Jackman, T.R. & Karanth K.P. (2014) Cryptic species and Miocene diversification of Palaearctic naked-toed geckos (Squamata: Gekkonidae) in the Indian dry zone. Zoologica Scripta, 43, 455–471.

Agarwal, I. & Karanth, K.P. (2015) A phylogeny of the only ground-dwelling radiation of *Cyrtodactylus* (Squamata, Gekkonidae): diversification of *Geckoella* across peninsular India and Sri Lanka. Molecular Phylogenetics and Evolution, 82, 193–199.

Agarwal, I., Khandekar, A., Giri, V.B., Ramakrishnan, U. & Karanth, K.P. (2019) The hills are alive with geckos! A radiation of a dozen species on sky islands across peninsular India (Squamata: Gekkonidae, *Hemiphyllodactylus*) with the description of three new species. Organisms Diversity and Evolution, 19, 341–361.

Agarwal, I. & Ramakrishnan, U. (2017) A phylogeny of open-habitat lizards (Squamata: Lacertidae: *Ophisops*) supports the antiquity of Indian grassy biomes. Journal of Biogeography, 44, 2021-2032.

Aitchison, J.C., Ali, J. R. & Davis, A. M. (2007) When and where did India and Asia collide? Journal of Geophysical Research, 112, B05423.

Ali, J.R. & Aitchison, J.C. (2008) Gondwana to Asia: Plate tectonics, paleogeography and the biological connectivity of the Indian subcontinent from the Middle Jurassic through latest Eocene (166–35 Ma). Earth-Science Reviews, 88, 145–166.

Arnold, E.N. & Poinar, G. (2008) A 100 million year old gecko with sophisticated adhesive toe pads, preserved in amber from Myanmar. Zootaxa, 1847, 62–68.

Austin, J.J., Arnold, E.N. & Jones, C.G. (2004) Reconstructing an island radiation using ancient and recent DNA: the extinct and living day geckos (*Phelsuma*) of the Mascarene islands. Molecular Phylogenetics and Evolution, 31, 109-22.

Bansal, R. & Karanth, K.P. (2010) Molecular phylogeny of *Hemidactylus* geckos (Squamata: Gekkonidae) of the Indian subcontinent reveals a unique Indian radiation and an Indian origin of Asian house geckos. Molecular Phylogenetics and Evolution, 57, 459-465.

Bansal, R. & Karanth, K.P. (2013) Phylogenetic analysis and molecular dating suggest that *Hemidactylus anamallensis* is not a member of the *Hemidactylus* radiation and has an ancient late Cretaceous origin. PLoS ONE, 8, e60615.

Blanford, W. (1901) Distribution of Vertebrate Animals in India, Ceylon, and Burma Philosophical Transactions of the Royal Society of London, 194, 335-436.

Bossuyt, F., Brown, R.M., Hillis, D.M., Cannatella, D.C. & Milinkovitch, M.C. (2006) Phylogeny and biogeography of a cosmopolitan frog radiation: Late Cretaceous diversification resulted in continent-scale endemism in the family Ranidae. Systematic Biology, 55, 579–594.

Bossuyt, F. & Milinkovitch, M.C. (2001) Amphibians as indicators of early Tertiary "Out-of-India" dispersal of vertebrates. Science, 292, 93–95.

Bocxlaer, I.V., Roelants, K., Biju, S.D., Nagaraju, J. & Bossuyt, F. (2006) Late Cretaceous vicariance in Gondwanan amphibians. PLoS ONE, 74,1–6.

Briggs, J.C. (1989) The historic biogeography of India: isolation or contact? Systematic Zoology, 38, 322–332.

Briggs, J.C. (2003) The biogeographic and tectonic history of India. Journal of Biogeography, 30, 381–388.

Brusatte, S.L., O'Connor, J.K & Jarvis, E.D. (2015) The origin and diversification of birds. Current Biology, 25, R888–R89.

Burbrink, F.T., Grazziotin, F.G., Pyron, R.A. et al. (2020) Interrogating genomic-scale data for Squamata (lizards, snakes, and amphisbaenians) shows

no support for key traditional morphological relationships. Systematic Biology, 69, 502–520.

Baxter, A.T., Aitchison, J.C., Ali, J.R., Chan, J.S-L. and Chan, G.H.N. (2016) Detrital chrome spinel evidence for a Neotethyan intra-oceanic island arc collision with India in the Paleocene. Journal of Asian Earth Sciences, 128, 90–104.

Chatterjee, S. & Scotese, C. (1999) The breakup of Gondwana and the evolution and biogeography of the Indian Plate. Proceedings of Indian National Science Academy, A65 397–425

Chatterjee, S., Scotese, C.R. & Bajpai, S. (2017) The restless Indian plate and its epic voyage from Gondwana to Asia: its tectonic, paleoclimatic, and paleobiogeographic evolution: Geological Society of America, Boulder, Colorado. USA.

Claramunt, S. & Cracraft, J. (2015) A new time tree reveals Earth history's imprint on the evolution of modern birds. Science Advances, 1, e1501005.

Clyde, W.C., Khan, I.H. & Gingerich, P.D. (2003) Stratigraphic response and mammalian dispersal during initial India-Asia collision: evidence from the Ghazij Formation, Balochistan, Pakistan. Geology, 31, 1097–1100.

Corbet, G.B. & Hill, J.E. (1992) The mammals of the Indomalayan Region: a systematic review. Oxford University Press, Oxford, UK.

Crottini, A., Madsenc, O., Poux, C., Strauß, A., Vieites, D.R. & Vences, M. (2012) Vertebrate time-tree elucidates the biogeographic pattern of a major biotic change around the K–T boundary in Madagascar. Proceedings of the National Academy of Sciences USA, 109, 5358–5363.

Cyriac, V.P. & Kodandaramaiah, U. (2018) Digging their own macroevolutionary grave: fossoriality as an evolutionary dead end in snakes. Journal of Evolutionary Biology, 31, 587–598.

Datta-Roy, A. & Karanth, K.P. (2009) The Out-of-India Hypothesis: what do molecules suggest? Journal of Biosciences, 34, 687-697.

Donoghue, M.J & Moore, B.R. (2003) Toward an integrative historical biogeography. Integrative and Comparative Biology, 43, 261–270.

Feduccia, A. (2003) 'Big bang' for tertiary birds? Trends in Ecology and Evolution, 18, 172-176.

Feng, Y.J., Blackburn, D.C., Liang, D., Hillis, D.M., Wake, D.B., Cannatella, D.C. & Zhang, P. (2017) Phylogenomics reveals rapid, simultaneous diversification of three major clades of Gondwanan frogs at the Cretaceous–Paleogene boundary. Proceedings of the National Academy of Sciences USA, 114, E5864–E5870.

Folie, A., Rana, R.S., Rose, K.D., Sahni, A., Kumar, K., Singh, L. & Smith, T. (2013) Early Eocene frogs from Vastan Lignite Mine, Gujarat, India. Acta Palaeontologica Polonica, 58, 511-524.

Gamble, T., Bauer, A.M., Colli, G.R., Greenbaum, E., Jackman, T.R., Vitt, L.J. & Simons, A. M. (2011) Coming to America: multiple origins of New World Geckos. Journal of Evolutionary Biology, 24, 231–244.

Gower, D.J., Kupfer, A., Oommen, O.V., et al. (2002) A molecular phylogeny of ichthyophiid caecilians (Amphibia: Gymnophiona: Ichthyophiidae): out of India or out of South East Asia? Proceedings of the Royal Society B, 269, 1563–1569.

Grismer, J.L., Schulte, II J.A., Alexander, A., Wagner, P., Travers S.L., Buehler, M.D., Welton, L.J. & Brown, R.M. (2016) The Eurasian invasion: phylogenomic data reveal multiple Southeast Asian origins for Indian Dragon Lizards. BMC Evolutionary Biology, 16, 43.

Harrington, S.M. & Reeder, T.W. (2017) Phylogenetic inference and divergence dating of snakes using molecules, morphology and fossils: new insights into convergent evolution of feeding morphology and limb reduction. Biological Journal of the Linnean Society, 121, 379–394.

Honda, M., Ota, H., Kohler, G., Eneich, I., Chirio, L., Chen, S. & Hikida, T. (2003) Phylogeny of lizard subfamily Lygosominae (Reptilia: Scincidae), with special reference to the origin of new world taxa. Genes and Genetic Systems, 78, 71–80.

Hsiang, A.Y., Field, D.J., Webster, T.H., Behlke, A.D.B., Davis, M.B., Racicot, R.A. & Gauthier, J.A. (2015) The origin of snakes: revealing the ecology, behavior, and evolutionary history of early snakes using genomics, phenomics, and the fossil record. BMC Evolutionary Biology, 15, 87.

Jana, A. & Karanth, P. (2019) Multilocus nuclear markers provide new insights into the origin and evolution of the blackbuck (Antilope cervicapra, Bovidae). Molecular Phylogenetics and Evolution, 139, 106560.

Jarvis, E.D., Mirarab, S., Aberer, A.J., et al. (2014) Whole-genome analyses resolve early branches in the tree of life of modern birds. Science, 346, 1320-1331.

Jonniaux, P. & Kumazawa, Y. (2008) Molecular phylogenetic and dating analyses using

mitochondrial DNA sequences of eyelid geckos (Squamata: Eublepharidae). Gene, 407, 105-115.

Joshi, J. & Karanth, K.P. (2011) Cretaceous-Tertiary diversification among select Scolopendrid centipedes of South India. Molecular Phylogenetics and Evolution, 60, 287–294.

Kamei, R.G., Mauro, D.S., Gower, D.J., et al. (2012) Discovery of a new family of amphibians from northeast India with ancient links to Africa. Proceedings of the Royal Society B, 279, 2396–2401.

Karanth, K.P. (2006) Out-of-India Gondwanan origin of some Asian biota. Current Science, 90, 789-792.

Karanth, K.P. (2015) An island called India: phylogenetic patterns across multiple taxonomic groups reveal endemic radiations. Current Science, 108, 1847-1851.

Karin, B.R., Metallinou, M., Weinell, J.L., Jackman, T.R. & Bauer, A.M. (2016) Resolving the higher-order phylogenetic relationships of the circumtropical *Mabuya* group (Squamata: Scincidae): an out-of-Asia diversification. Molecular Phylogenetics and Evolution, 102, 220-232.

Khajuria, C.K. & Prasad, G.V.R. (1998) Taphonomy of a Late Cretaceous mammal-bearing microvertebrate assemblage from the Deccan inter-trappean beds of Naskal, peninsular India. Palaeogeography, Palaeoclimatology, Palaeoecology, 137, 153-172.

Khosla, A & Sahni, A. (2003) Biodiversity during the Deccan volcanic eruptive episode. Journal of Asian Earth Science, 21, 895–908.

Kimball, R.T., Oliveros, C.H., Wang, N., et al. (2019) A phylogenomic supertree of birds. Diversity, 11, 109.

Krosch, M.N., Schutze, M.K., Armstrong, K.F., Graham, G.C., Yeates, D.K. & Clarke, A.R. (2012) A molecular phylogeny for the Tribe Dacini (Diptera: Tephritidae): systematic and biogeographic implications. Molecular Phylogenetics and Evolution, 64, 513-523.

Lawson, R., Slowinski, J.B., Crother, B.I. & Burbrink, F.T. (2005) Phylogeny of the Colubroidea (Serpentes): new evidence from mitochondrial and nuclear genes. Molecular Phylogenetics and Evolution, 37, 581–601.

Liu, L., Zhang, J., Rheindt, F.E., et al. (2017) Genomic evidence reveals a radiation of placental mammals uninterrupted by the KPg boundary. Proceedings of the National Academy of Sciences USA, 114, E7282–E7290.

Longrich, N.R., Bhullar, B.-A.S. & Gauthier, J.A. (2012) Mass extinction of lizards and snakes at the Cretaceous–Paleogene boundary. Proceedings of the National Academy of Sciences USA, 109, 21396–21401.

Longrich, N.R., Tokaryk, T. & Field, D.J. (2011) Mass extinction of birds at the Cretaceous–Paleogene (K–Pg) boundary. Proceedings of the National Academy of Sciences, USA, 108, 15253-15257.

Macey, J.R., Schulte, J.A., Larson, A., Ananjeva, N.B., Wang, Y., Pethiyagoda, R., Rastegar-Pouyani, N. & Papenfuss, T.J. (2000) Evaluating trans-tethys migration: an example using acrodont lizard phylogenetics. Systematic Biology, 49, 233–256.

Mani, M.S. (1974) Biogeographical evolution in India. In: Ecology and Biogeography of India, (ed. by M.S. Mani) pp. 698–724. W. Junk, The Hague.

Miralles, A., Marin, J., Markus, D., Herrel, A., Hedges, S.B. & Vidal, N. (2018) Molecular evidence for the paraphyly of Scolecophidia and its evolutionary implications. Journal of Evolutionary Biology, 31, 1782-1793.

Noonan, B.P. & Chippindale, P.T. (2006a) Dispersal and vicariance: the complex evolutionary history of boid snakes. Molecular Phylogenetics and Evolution, 40, 347–358.

Noonan, B.P. & Chippindale, P.T. (2006b) Vicariant origin of Malagasy reptiles supports Late Cretaceous Antarctic land bridge. American Naturalist, 168, 730–741.

Oaks, J.R. (2011) A time-calibrated species tree of Crocodylia reveals a recent radiation of the true crocodiles. Evolution, 65, 3285-3297.

Pereira, A.G., Sterli, J., Moreira, F.R.R. & Schrago, C.G. (2017) Multilocus phylogeny and statistical biogeography clarify the evolutionary history of major lineages of turtles. Molecular Phylogenetics and Evolution, 113, 59–66.

Prasad, G.V.R. & Sahni, A. (2009) Late Cretaceous continental vertebrate fossil record from India: palaeobiogeographical insights. Bulletin de la Société Géologique de France, 180, 369-381.

Prum, R., Berv, J., Dornburg, A., Field, D., Townsend, J., Lemmon, E. & Lemmon, A. (2015) A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. Nature. 526, 569–573.

Pyron, R.A., Burbrink, F.T. & Wiens, J.J. (2013) A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC Evolutionary Biology, 13, 93.

Rage, J.–C., Folie, A., Rana, R.S., Singh, H., Rose, K.D. & Smith, T. (2008) A diverse snake fauna from the early Eocene of Vastan Lignite Mine, Gujarat, India. Acta Palaeontologica Polonica, 53, 391–403.

Rana, R.S., Augé, M., Folie, A., Rose, K.D., Kumar, K., Singh, L., Sahni A. & Smith, T. (2013) High diversity of acrodontan lizards in the Early Eocene Vastan Lignite Mine of India. Geologica Belgica, 16, 290-301.

Raven, P.H. & Axelrod, D.I. (1974) Angiosperm biogeography and past continental movements. Annals Missouri Botanical Garden, 61, 539–673.

Raxworthy, C.J., Forstner, M.R.J. & Nussbaum, R.A. (2002) Chameleon radiation by oceanic dispersal. Nature, 415, 784-787.

Renne, P.R., Sprain, C.J., Richards, M.A., Self, S., Vanderkluysen, L. & Pande, K. (2015) State shift in Deccan volcanism at the Cretaceous-Paleogene boundary, possibly induced by impact. Science, 350, 76-78.

Reynolds, R.G., Niemiller, M.L. & Revell, L.J. (2014) Toward a Tree-of-Life for the boas and pythons: multilocus species-level phylogeny with unprecedented taxon sampling. Molecular Phylogenetics and Evolution, 71, 201–213.

Roelants, K., Gower, D.J., Wilkinson, M., Loader, S.P., Biju, S.D., Guillaume, K., Moriau, L. & Bossuyt, F. (2007) Global patterns of diversification in the history of modern amphibians. Proceedings of the National Academy of Sciences USA, 104, 887–892.

Schoene, B., Samperton, K.M., Eddy, M.P. et al. (2015) U-Pb geochronology of the Deccan Traps and relation to the end-Cretaceous mass extinction. Science, 347, 182-184.

Sil, M., Aravind, N.A. & Karanth, K.P. (2020) Into-India or out-of-India? Historical biogeography of the freshwater gastropod genus Pila (Caenogastropoda: Ampullariidae). Biological Journal of the Linnean Society, 129, 752–764.

Simões, T.R., Caldwell, M.W., Tałanda, M., Bernardi, M., Palci, A., Vernygora, O., Bernardini, F., Mancini, L. & Nydam, R.L. (2018) 2018. The origin of squamates revealed by a Middle Triassic lizard from the Italian Alps. Nature, 557, 706-709.

Smith, T., Kumar, K., Rana, R.S., Folie, A., Solé, F., Noiret, C., Steeman, T., Sahni, A. & Rose, K.D. (2016) New early Eocene vertebrate assemblage from western India reveals a mixed fauna of European and Gondwana affinities. Geoscience Frontiers, 7, 969-1001.

Sprain, C.J., Renne, P.R., Vanderkluysen, L., Pande, K., Self, S. & Mittal, T. (2019) The eruptive tempo of Deccan volcanism in relation to the Cretaceous-Paleogene boundary. Science, 363, 866–870.

Tarver, J.E., Reis, M.d., Mirarab, S., et al. (2016) The interrelationships of placental mammals and the limits of phylogenetic inference. Genome Biology and Evolution, 8, 330–344.

Thewissen, J.G.M. & McKenna, M.C. (1992) Paleobiogeography of Indo-Pakistan: a response to Briggs, Patterson, and Owen. Systematic Biology, 41, 248-251.

Tolley, K.A., Townsend, T.M. & Vences, M. (2013) Large-scale phylogeny of chameleons suggests African origins and Eocene diversification. Proceedings of the Royal Society B, 280, 20130184.

Toussaint, E.F.A., Fikacek, M. & Short, A.E.Z. (2016) India–Madagascar vicariance explains cascade beetle biogeography. Biological Journal of the Linnean Society, 118, 982–991.

Upham, N.S., Esselstyn, J.A. & Jetz, W. (2019) Inferring the mammal tree: species-level sets of phylogenies for questions in ecology, evolution, and conservation. PLoS Biology 17, e3000494.

Vences, M., Freyhof, J., Sonnenberg, R., Kosuch, J. & Veith, M. (2001) Reconciling fossils and molecules: Cenozoic divergence of cichlid fishes and the biogeography of Madagascar. Journal of Biogeography, 28, 1091-1099.

Vences, M. (2004) Origin of Madagascar's extant fauna: a perspective from amphibians, reptiles and other non-flying vertebrates. Italian Journal of Zoology, 71, 217-228.

Vences, M., Wanke, S., Vieites, D.R., Branch, W.R., Glaw, F. & Meyer, A. (2004) Natural colonization or introduction? Phylogeographical relationships and morphological differentiation of house geckos (Hemidactylus) from Madagascar. Biological Journal of the Linnean Society, 83, 115–130.

Vidal, N., Delma, A.-S. & Hedges, S.B. (2007) The higher-level relationships of Alethinophidian

snakes inferred from seven nuclear and mitochondrial genes. In: Biology of the Boas and Pythons, (ed. by R.W. Henderson and R. Powell) pp. 27-33. Eagle Mountain Publishing Inc., UT, USA.

Vidal, N., Marin, J., Morini, M., Donnellan, S., Branch, W.R., Thomas, R., Vences, M., Wynn, A., Cruaud, C. & Hedges, S.B. (2010) Blindsnake evolutionary tree reveals long history on Gondwana. Biology Letters, 6, 558–561.

Vidal, N., Marin, J., Sassi, J., et al. (2012) Molecular evidence for an Asian origin of monitor lizards followed by Tertiary dispersals to Africa and Australasia. Biology Letters, 8, 853–855.

Wallace, A. (1876) The geographical distribution of animals: with a study of the relations of living and extinct faunas as elucidating the past changes of the earth's surface. Cambridge University Press, Cambridge.

Whiting, A.S., Sites, J.W. & Bauer, A.M. (2004) Molecular phylogenetics of Malagasy skinks (Squamata: Scincidae). African Journal of Herpetology, 53, 135-146.

Wilkinson, M., Sheps, J.A., Oommen, O.V. & Cohen, B.L. (2002) Phylogenetic relationships of Indian caecilians (Amphibia: Gymnophiona) inferred from mitochondrial rRNA gene sequences. Molecular Phylogenetics and Evolution, 23, 401–407.

Yoder, A.D. & Nowak, M.D. (2006) Has vicariance or dispersal been the predominant biogeographic force in Madagascar? Only time will tell. The Annual Review of Ecology, Evolution, and Systematics, 37, 405–31.

Zhang, P., Papenfuss, T.J., Wake, M.H., Qu, L. & Wake, D.B. (2008) Phylogeny and biogeography of the family Salamandridae (Amphibia: Caudata) inferred from complete mitochondrial genomes. Molecular Phylogenetics and Evolution, 49, 586–597.

Zheng, Y. & Wiens, J.J. (2016) Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. Molecular Phylogenetics and Evolution, 94, 537–547.