Faunal similarity in Madagascan and South Indian Late Cretaceous vertebrate faunas

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ABSTRACT

The modern-day fauna of the Indian subcontinent is a mixture of ancestral Gondwanan clades, Laurasian immigrants, and endemic radiations as a result of its complex geological history. During the latest Cretaceous, the Indian subcontinent has been reconstructed at peak isolation from other continents, having separated last from Madagascar approximately 85 million years ago. The majority of vertebrate fossils known from the Late Cretaceous of India are from the Deccan Volcanic Province, but fossil material from the Cauvery Basin in South India has provided a second diverse vertebrate fauna from this time period. Here, we use the modified Forbes and Raup-Crick faunal dissimilarity indices to demonstrate that the faunal composition of the Cauvery Basin is distinct from that of the Deccan intertrappean and infratrappean beds, and shows greater faunal similarity with the Maevarano Basin of Madagascar than other Indian localities, despite several million years having elapsed since the geological separation of the two island continents.

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1. Introduction

After the break-up of Eastern Gondwana was initiated approximately 160 million years ago (Ma) (Gibbons et al., 2013), India and Madagascar remained geologically connected until 84–96 Ma (Storey et al., 1995; Storey et al., 1997; Sampson et al., 1998; Briggs, 2003; Melluso et al., 2009). Subsequent to the separation of India and Madagascar, they existed as isolated island continents during most of the Late Cretaceous and early Cenozoic, until India contacted Eurasia about 47 Ma (Matthews et al., 2016, although see discussion of dates therein). The palaeogeographic history of India – first as an integral part of Gondwana, followed by nearly 40 million years of isolation, and finally contact with Laurasia – has led to a patchwork set of biogeographic relationships within India's flora and fauna. In the present day, Indian taxa are a mixture of clades with Gondwanan origins, endemic Indian radiations, and Laurasian immigrants (e.g. Mani, 1974; Datta-Roy and Karanth, 2009; van Bocxlaer et al., 2009; Karanth, 2015).

Madagascar has remained isolated, but in closer proximity to other Gondwanan landmasses, particularly Africa. As a result, the island today possesses one of the highest degrees of endemism of anywhere in the world (Goodman and Benstead, 2005; Whittaker and Fernández-Palacios, 2007). Many of these endemically radiating clades

derive primarily from Cenozoic dispersal events from other Gondwanan landmasses, particularly Africa (Yoder and Nowak, 2006), with the effects of the island's palaeogeographic history still apparent today (Samonds et al., 2013). Both Madagascar and India share large numbers of family-level taxa with contemporaneous strata in South America, suggesting some degree of cosmopolitanism and vicariance in the paleobiogeographic history of Gondwanan clades (Krause et al., 1997; Krause et al., 2006; Ali and Krause, 2011).

Late Cretaceous fossils in India are known primarily from two regions: the Deccan Volcanic Province (hereafter DVP) and the Cauvery Basin. The DVP extends over 500,000 km² of western central India (Mahoney, 1989), and represents 750,000 years of sporadic volcanic eruption, 80% of which took place over tens of thousands of years beginning in the magnetic chron immediately preceding the K-Pg boundary (Chenet et al., 2008; Chenet et al., 2009) and, for this reason, has often been suggested as a possible driver of the end-Cretaceous mass extinction (Keller et al., 2011). Fossils in the DVP are known both from sediments pre-dating the advent of volcanism – the 'infratrappean beds', including the wide-ranging Lameta Formation – and from thin layers of sedimentary rock deposited between periods of volcanic activity – the 'intertrappean beds'. The majority of work on Late Cretaceous Indian faunas has concerned these infra- and intertrappean beds (see review in Prasad, 2012).

The second major outcrop of fossiliferous Late Cretaceous rock in India is found in the Cauvery Basin, an extensive series of marine, coastal, and fluvial-deltaic formations in the South East Indian state of Tamil

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Nadu. The Cauvery Basin as a whole contains rocks from the Early Cretaceous to the Miocene (Sundaram et al., 2001) with multiple regression events recorded from the Late Cretaceous through the Cenozoic. Vertebrate fossils have been known from the Cauvery Basin since the 19th century (Egerton, 1845; Blanford, 1862; Lydekker, 1877), with diverse vertebrate faunas known predominantly from two formations – the Albian to Turonian Karai Formation (Underwood et al., 2011; Verma et al., 2012) and the Late Maastrichtian Kallamedu Formation (Gaffney et al., 2001; Prasad et al., 2013; Goswami et al., 2013).

Both the vertebrate faunas of the DVP and the Cauvery Basin contain several clades with pan-Gondwanan distributions. The DVP has yielded abelisaurid dinosaurs (e.g. Wilson et al., 2003), bothremydid turtles (Carter, 1852; Jain, 1986; Gaffney et al., 2003; de Lapparent de Broin et al., 2009), nigerophiid and madtsoiid snakes (e.g. Rage and Prasad, 1992; Rage et al., 2004; Wilson et al., 2010; Mohabey et al., 2011), and gondwanatherian mammals (Krause et al., 1997; Prasad et al., 2007), while the Cauvery Basin has also yielded gondwanatherians (Goswami et al., 2012) and abelisaurids, as well as a simosuchid crocodyliform (Prasad et al., 2013).

Additionally, there are in each of DVP and the Cauvery Basin a small number of clades with primarily Laurasian affinities, such as pelobatid and discoglossid frogs (Sahni et al., 1982), anguimorph lizards (Prasad and Rage, 1995), eutherian mammals in the intertrappean beds of southern and central DVP (Prasad and Sahni, 1988; Boyer et al., 2010), as well as a troodontid theropod dinosaur (Goswami et al., 2013), and phyllodontid fish toothplates (Halliday et al., 2016) from the Cauvery Basin in South India.

The relatively new discoveries from the Cauvery Basin raise the question of provinciality in India's Late Cretaceous fauna, which has otherwise been studied almost exclusively in the DVP. The new fauna described from the Cauvery Basin also suggests extensive similarity with Late Cretaceous Madagascan localities nearly 20 million years after the separation of these two landmasses. We here calculate metrics of faunal similarity for all Late Cretaceous localities in India and Madagascar, to identify whether the composition of taxa discovered in each locality are drawn from the same overarching population, or whether there were distinct faunal zones within the Indo-Madagascan region at the end of the Mesozoic. Specifically, we compare taxonomic occurrence data at locality and regional levels to identify any structure in the faunal composition of different localities.

2. Materials and methods

2.1. Occurrence data

Vertebrate occurrence data from all Late Cretaceous (Cenomanian to Maastrichtian) sites across India and Madagascar were compiled from the literature and from the Paleobiology Database (www.paleobiodb.org, accessed 30th Mar 2016). Further occurrences from our recently published (Halliday et al., 2016) and unpublished data (e.g. those taxa mentioned in Goswami et al., 2012 but not yet formally described) were also included. Taxonomic information was compiled at the family, genus, and species level. Where possible, formations were divided. The Maevarano Formation of Madagascar was split into the well-characterised Lac Kinkony member and a composite of the Anembalemba, Masorobe, and Miadana localities, which cannot reliably be distinguished (D.W. Krause, pers comm. 2016). Here, that composite is referred to simply as Maevarano. The infratrappean and intertrappean beds of the Deccan Volcanic Province were also separated by locality. In total, 553 taxon occurrences comprising 73 identifiable families were combined across 43 localities (Supplementary File 1), of which 38 contained at least one specimen identifiable to family level. Individual
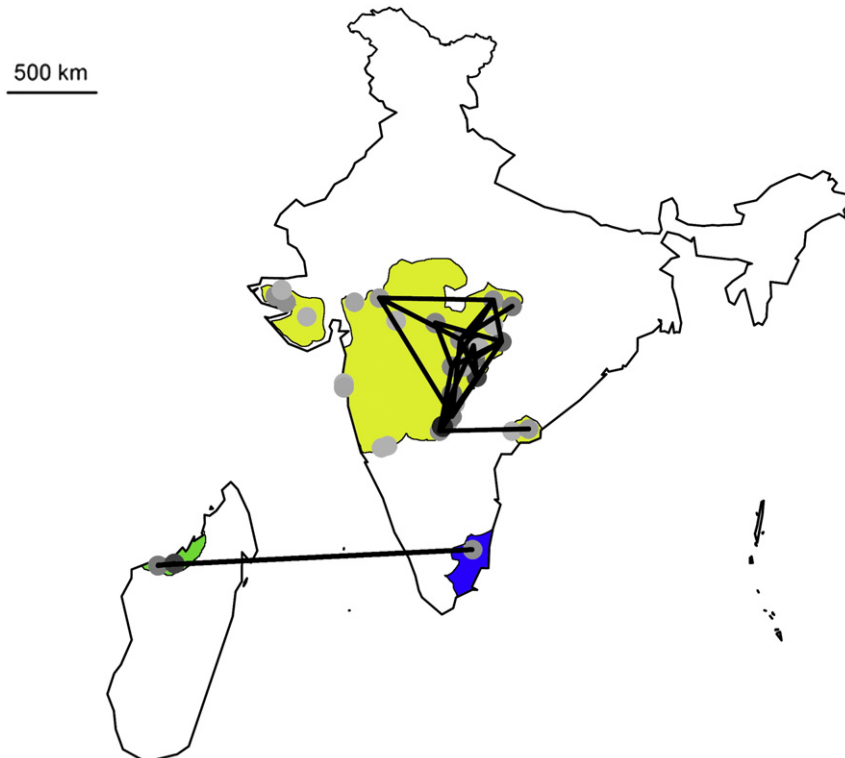

Fig. 1. Significant faunal similarity among Indian and Madagascan Late Cretaceous localities according to the Raup-Crick index. Circles are the present day locations of Late Cretaceous fossil sites, with the colour corresponding to the number of identifiable families known from that locality, from grey (1 family) to black (33 families). Lines connecting localities represent pairs of sites with significantly similar faunas, for faunas with at least five taxa. Three regions are depicted: the DVP, comprising inter- and infratrappean beds (yellow), the Cauvery Basin (blue) and the Maevarano Formation (green). Many of the Central Indian intertrappean and infratrappean beds contain significantly similar species to one another, but there is no similarity between Southern India and Central India, or between Central India and Madagascar. Instead, the Kallamedu Formation is significantly similar to the Madagascan Lac Kinkony Member. Positions of India and Madagascar are not to scale.

Table 1

A summary of all significant similarities and dissimilarities between locality, divided into region and by dissimilarity index. ANJ = Anjar Pit, ASI = Asifabad, DEO = Deothan/Kheri, DON = Dongargaon, GUR = Gurmatkal, JAB = Jabalpur, MAE = Maevarano, MAR = Marepalli, KAC = Kachchh, KAL = Kallamedu, KIS = Kisalpuri, LAC = Lac Kinkony, LAM = Lameta, LOT = Lotkheri, NAG = Nagpur, NAS = Naskal, NIZ = Nizamabad, PIP = Piplanarayanwar, PIS = Pisdura, RAJ = Rajamundry, RAN = Rangapur.

			Intertrappean	Infratrappean	Cauvery	Madagascar
Raup-Crick	Similar	Intertrappean	ASI – MAR ASI – NAG ASI – PIP ASI – RAN GUR – RAJ KIS – PIP LOT – MAR LOT – PIP MAR – PIP NAG – NIZ NAS – NIZ NAS – RAN NIZ – RAN			
		Infratrappean	DON – DEO DON – GUR DON – MAR DON – RAN JAB – LOT JAB – PIP LAM – DEO LAM – GUR	DON – JAB DON – LAM DON – PIS JAB – LAM		
		Cauvery	-	-	-	
		Madagascar	-	-	LAC – KAL	LAC – MAE
	Dissimilar	Intertrappean	ANJ – ASI ANJ – RAJ ASI – KAC			
		Infratrappean	-	-		
		Cauvery	KAL – ANJ KAL – ASI KAL – GUR KAL – NAG KAL – NAS KAL – NIZ KAL – RAJ KAL – RAN	-	-	
		Madagascar	LAC – ASI LAC – GUR LAC – MAR LAC – NAG LAC – NAS LAC – NIZ LAC – RAJ LAC – RAN MAE – ASI MAE – DEO MAE – GUR MAE – NAG MAE – NAS MAE – NIZ MAE – RAJ MAE – RAN	LAC – DON LAC – PIS	-	-
Forbes	Similar	Intertrappean	LOT – NAS NAS – NIZ NAS – PIP			
		Infratrappean	-	-		
		Cauvery	-	-	-	
		Madagascar	-	-	-	LAC – MAE
	Dissimilar	Intertrappean	ANJ – RAJ			
		Infratrappean	-	-		
		Cauvery	KAL – ANJ KAL – GUR KAL – NIZ KAL – RAJ	-	-	
		Madagascar	LAC – GUR LAC – NIZ LAC – RAJ	-	-	-

The majority of Indian and Madagascan Late Cretaceous vertebrate localities have been interpreted as fluvial, fluvio-deltaic, alluvial, or lacustrine. Recent biostratigraphic analysis has determined that at least part of the Pondicherry-Ariyalur subgroup of the Cauvery Basin can be correlated temporally with the marine Berivotra Formation in Madagascar, as well as with periods of Deccan volcanism (Keller et al., 2016), meaning that the four regions are more or less temporally equivalent. As individual traps are not correlated across the DVP, many infratrappean beds may be younger than some intertrappean beds, despite placement. However, all localities included in this analysis are considered to be Maastrichtian in age.

2.2. Data analysis

Pairwise measures of faunal dissimilarity were conducted using two indices. Firstly, we used the Raup-Crick index (Raup and Crick, 1979), improved to allow additional testing of significant similarity (Chase et al., 2011). For each pair of localities, the modified Raup-Crick index generates a number between −1 and 1. If a pair of localities has a Raup-Crick index below −0.95, they are considered to be significantly similar in their faunal composition. If they have a value of above 0.95, they are considered to be significantly dissimilar – that is, the localities (samples) are drawn from significantly different faunas (populations). A total of 703 pairwise comparisons were conducted at the locality level, with an additional 6 at the regional level.

Secondly, we used the Forbes index (Forbes, 1907), which better accounts for variation in sample sizes, again modified and improved to better reflect overall similarity (Alroy, 2015a, 2015b). The Forbes index returns a number between 0 (where no taxa are shared between the sites) and 1 (where the taxon list is identical, or one is a subset of the other). Both modified Raup-Crick and corrected Forbes indices compare the observed shared number of species between two sites with the expected number from a null hypothesis that both species lists are derived from the same population.

Faunal similarity measures were calculated for each pair of localities, generating a faunal similarity distance matrix for each metric. Hierarchical cluster analyses were conducted using Ward's method (Ward, 1963) at both locality and regional level, in order to identify broader levels of faunal similarity across localities.

All analysis was conducted in R (R Development Core Team, 2010), using 'vegan' (Dixon, 2003) and code for calculating both modified Raup-Crick and Forbes pairwise dissimilarity matrices freely available online (bio.mq.edu.au/~jalroy/Forbes.R, retrieved 01/11/2016, http://www.esapubs.org/archive/ecos/C002/002/Raup-Crick.txt, retrieved 01/11/2016).

3. Results

Several localities contained few or single families of vertebrates. As the corrected Forbes method returns a value of 1 when one fauna is a subset of another, this resulted in very high numbers of significantly similar faunas. Details of all such pairwise comparisons may be found in the supplementary information (Supplementary File 2), but here we restrict discussion to comparisons between those faunas from which five or more families have been retrieved. Twelve pairwise combinations of localities containing more than five family-level groups of vertebrates were found to be significantly different using the Raup-Crick metric. In all twelve of these, an intertrappean or infratrappean bed was significantly dissimilar to a Madagascan or Cauvery Basin locality. Twenty-four pairwise comparisons showed significant similarities between faunas under the Raup-Crick metric (Fig. 1, Table 1). Thirteen of these were within regional groups, and a further ten were between intertrappean and infratrappean localities in the DVP. However, one pair of localities showed significant similarity between Madagascar and India: the Lac Kinkony Member of the Maevarano Formation in Madagascar was significantly similar to the Kallamedu Formation of

localities were grouped to form four palaeogeographic and stratigraphic regions: Madagascar, the Cauvery Basin, the DVP infratrappean beds, and the DVP intertrappean beds (Fig. 1).

the Cauvery Basin. There were no significant similarities between the Kallamedu Formation and any bed of the Deccan Volcanic Province. All significant pairwise comparisons, similar and dissimilar, are listed in Table 1.

When pairwise comparisons were made using the corrected Forbes metric of dissimilarity, only four comparisons between localities with five or more families present showed significant similarity (Forbes values above 0.95): Naskal and Nizamabad; Naskal and Lotkheri; Naskal and Piplanarayanwar; Lac Kinkony and Maevarano. Three of the four are pairs of intertrappean beds with relatively high faunal richness. The remaining pair is of the two Madagascan localities. Eight pairwise comparisons were significantly dissimilar under the modified Forbes metric. Seven of these dissimilarities are between the Cauvery Basin or Madagascar and the DVP.

In the cluster analyses, the faunas of the Cauvery Basin most resembled those of the Maevarano Formation when grouped according to region (Fig. 2, Supplementary File 3), separately from a group of infra- and intertrappean beds of the DVP. At locality level, the Kallamedu Formation once again clustered with the separated Lac Kinkony and Maevarano localities. All of these relationships demonstrate a close similarity between the Cauvery Basin and the Maevarano Formation.

4. Discussion

A connection between Madagascar and India during the Late Cretaceous has been hypothesised through the Seychelles Plateau (Patriat and Segoufin, 1988) – a series of volcanic islands that would have provided a route through which a series of short distance dispersal events would have allowed connection between these habitats (Rage, 1996). In the context of the present study, similarity between the Kallamedu and Maevarano Formations, but not with the DVP, supports a hypothesis of transoceanic dispersal of terrestrial and freshwater (and perhaps shallow marine) taxa across the series of islands, rather than an ancestrally homogenous taxonomic composition. Alternatively, the faunas of South India and Madagascar may have been shared prior to their geological separation, with a distinct fauna in Central India. This latter explanation can only be true if the distinction between South and Central Indian faunas was maintained for the 20 million years between separation of India and Madagascar and the deposition of the Kallamedu and Maevarano Formations. As the Late Cretaceous faunas of India,

Madagascar, and South America include the same basic group of family-level taxa (Krause et al., 2006), such a vicariance hypothesis is certainly plausible.

That there was significant faunal similarity among many intertrappean localities suggests that each of those intertrappean beds can be considered to be a sample drawn from the same overall population. These localities are geographically widespread, across a large proportion of present day central and south-central India.

The significant faunal dissimilarity between the Kallamedu Formation and several intertrappean localities indicates that South India was ecologically distinct at the time of the Deccan volcanism. Even when considering larger-scale provinces as a whole, the Cauvery Basin remains consistently more similar in faunal similarity to Late Cretaceous Madagascar than to the DVP. Based on biogeographic patterns in extant taxa, it has previously been suggested that the southern Western Ghats of India acted as refugia for at least some taxa during the period of Deccan volcanic activity (Joshi and Karanth, 2013). If the faunas of successive intertrappean beds were derived from migrations from some external refugium, it would be expected that the taxic composition of the intertrappean beds would represent a subsample of the fauna of that refugium. Although this is not directly testable for the southern Western Ghats due to a lack of Cretaceous and early Cenozoic outcrops in that region, the southern refugium hypothesis (A in Fig. 3) can be rejected for at least the Cauvery Basin. The latest Cretaceous Kallamedu Formation, contemporaneous with the Deccan basalts, comprises a fauna drawn from a significantly different population of taxa, particularly when considering those taxa present in the Cauvery Basin and but absent from any DVP locality, such as a troodontid dinosaur and a simosuchid crocodylomorph. For the same reason, it cannot be said that the Cauvery Basin and DVP represent local variations of the same fauna (C in Fig. 3). Alternative palaeobiogeographic scenarios that are consistent with the data include vicariance from a common South Indian-Madagascan ancestral fauna (B in Fig. 3) or dispersal between South India and Madagascar (D in Fig. 3 with limited north-south Indian dispersal).

5. Conclusions

India and Madagascar share a large number of families, including abelisaurid theropods, sudamericid gondwanatherians, lepisosteid,
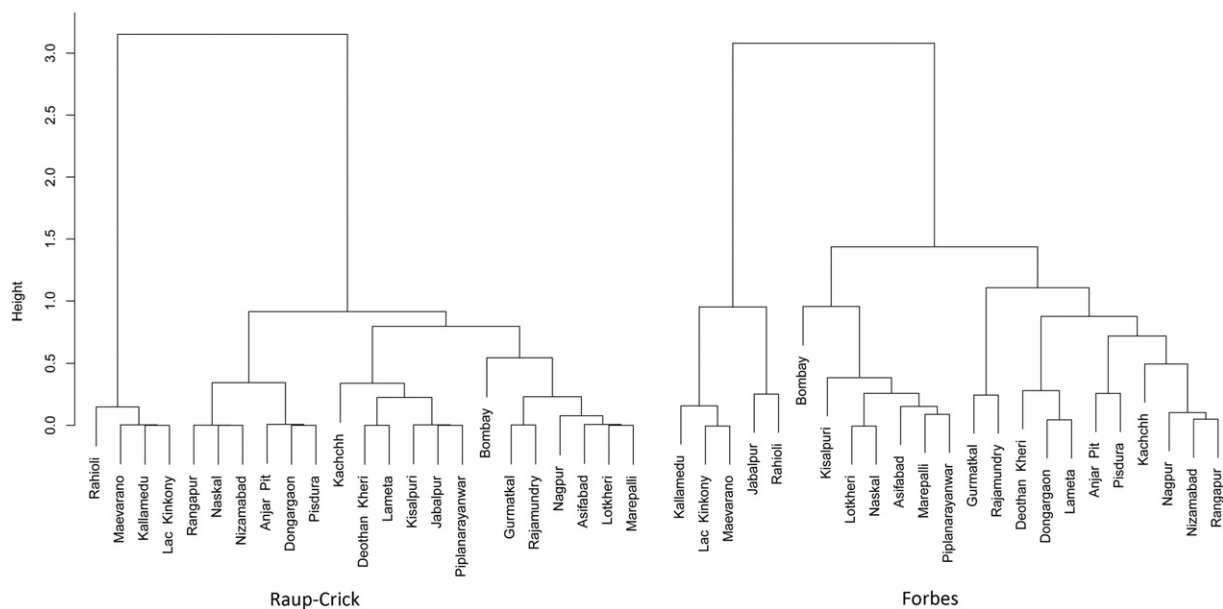

Fig. 2. Results of cluster analysis of Indian and Madagascan regional faunas. Using Raup–Crick or Forbes similarity as a distance measure, the Kallamedu Formation clusters with a group comprising the Lac Kinkony and Maevarano localities, as well as the Rahioli infratrappean beds, which has yielded solely dinosaurian taxa such as abelisaurids and titanosaurids also known from Madagascar.
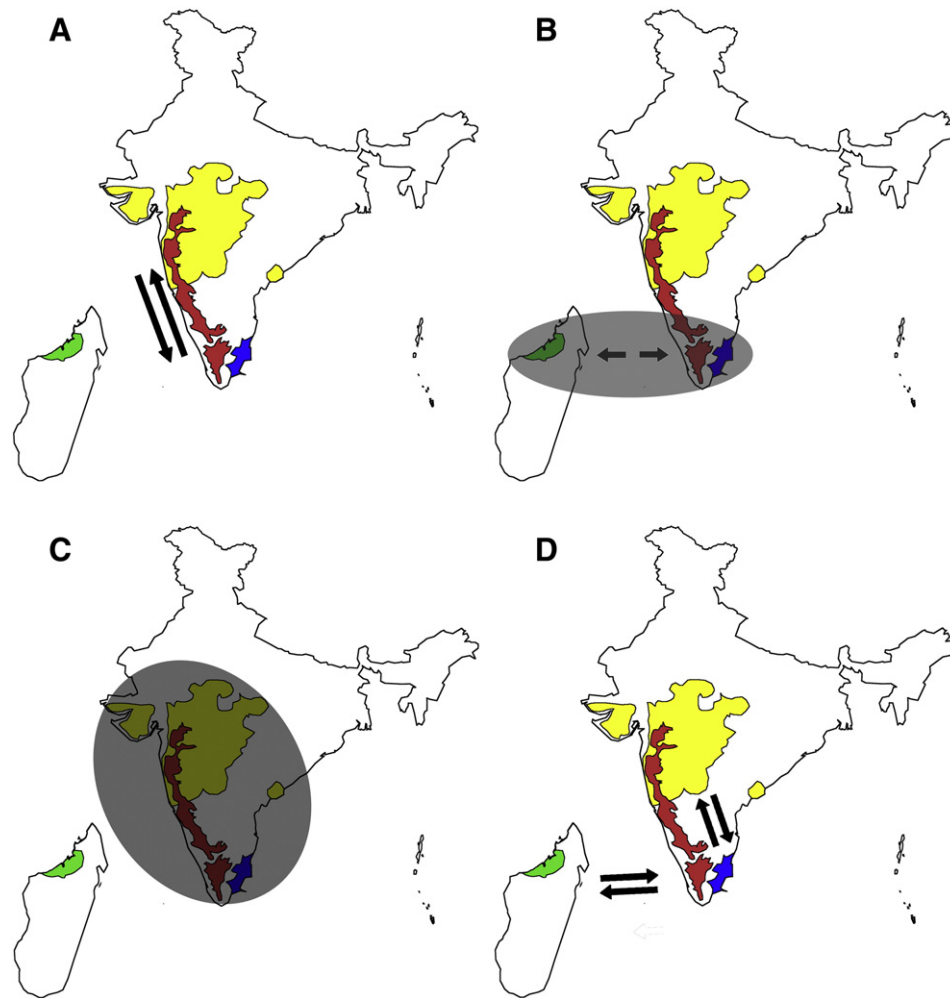
Fig. 3. Summary of Biogeographic Hypotheses. A – The Southern Refugium hypothesis of Joshi and Karanth (2013), in which southern India acted as a refugium of biodiversity during the ecological disturbance of the Deccan eruptions based around the Western Ghats. B – Vicariance of an Indian-Madagascan fauna. C – Presence of a single fauna across Maastrichtian Indian localities, of which the Cauvery Basin and DVP localities are samples. D – Dispersal between regions with the Cauvery Basin as an intermediate geographical area. Madagascan-Indian dispersal occurs over the Seychelles Plateau (Patriat and Segoufin, 1988). The DVP is coloured in yellow, the Cauvery Basin in blue, the Maevarano Formation in green, and, for a geographical comparison, Western Ghats in red. Positions of India and Madagascar are not to scale.

albulid, and phyllodontid teleosts, bothremydid turtles, and nigerophiid and madtsoiid snakes. The faunas of South India are, however, significantly different from the inter- and infratrappean beds of Central India. The fauna of the South Indian Kallamedu Formation of the Cauvery Basin are taxonomically more similar to Madagascan than to Central Indian localities, despite geographic separation of Madagascar and India for the previous 20 million years, and in spite of environmental similarity between South and Central Indian fossil localities. The Cauvery Basin of South India therefore represents a contemporaneous but distinct fauna from that of the intertrappean beds, revealing complexity in the patterning of species distributions in the Indian subcontinent throughout the Late Cretaceous.

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