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# Leaving Gondwana: The Changing Position of the Indian Subcontinent in the Global Faunal Network

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## ABSTRACT

The paleogeographic history of the Indian subcontinent is unique among Earth's landmasses. From being part of the southern supercontinent Gondwana for most of the Mesozoic, through a period of isolation as a drifting entity in the Late Cretaceous, to colliding with Asia near the Paleocene-Eocene boundary, the Indian subcontinent has been associated with, and dissociated from, a variety of landmasses. This paleogeographic history has been invoked to explain aspects of the subcontinent's modern-day fauna, with a combination of endemic radiations, remnants from Gondwana, and more recent immigrants from Laurasia. Here,

network approaches document how vertebrate faunas of the Indian subcontinent, and specifically their relationships to those of other landmasses, changed during the subcontinent's isolation from close faunal relationships with Madagascar and South America in the Late Cretaceous to a more Laurasian fauna most similar to those of Europe by the Eocene.

## INTRODUCTION

Among Earth's modern landmasses, the Indian subcontinent has arguably had the most complex paleobiogeographic history. Part of the massive southern supercontinent Gondwana for most of the Mesozoic, and particularly closely associated with Madagascar, Africa, Antarctica and Australasia, it sequentially separated from these landmasses and drifted northwards (Norton and Sclater, 1979; Powell, 1979; Subrahmanya, 1998; Ali and Aitchison, 2008; Chatterjee et al., 2013; Chatterjee et al., 2017). The precise timing and pattern of separation of the Gondwanan continents is not universally agreed upon, but the Indian subcontinent appears to have entirely separated from Madagascar by 84–92 Ma (Storey et al., 1995; Storey et al., 1997; Torsvik et al., 2000; Yatheesh et al., 2006), and remained isolated in the Indian Ocean throughout the rest of the Late Cretaceous and the entire Paleocene. Near the Paleocene-Eocene boundary, the Indian subcontinent finally collided with mainland Asia (Najman et al., 2010; Gibbons et al., 2015; Hu et al., 2016; Matthews et al., 2016), allowing for the possibility of biotic exchange (Briggs, 2003; Ali and Aitchison, 2008; Bajpai, 2009; Klaus et al., 2016). The position of India from the Cretaceous to the Eocene, as well as the location of all sites mentioned in this chapter, are found in Figures 1-3. Despite its increasingly well-documented, though still controversial, geophysical history, there remain certain aspects of the biogeographic history of the Indian subcontinent that render the pattern more complex. Throughout the subcontinent's isolation, oceanic islands and island arcs have

been hypothesized to link, directly or indirectly, the Indian subcontinent with Asia, Madagascar, Antarctica, South America, and Africa, potentially allowing faunal exchange among these landmasses. The Kerguelen Plateau (Krause et al., 1997; Sampson et al., 1998; Hay et al., 1999), the Chagos-Laccadive Ridge and Seychelles-Mascarene Plateau (Sahni, 1984; Ali and Aitchison, 2008), the Gunnerus Ridge (Case, 2002), and the Kohistan-Ladakh island-arc system (Chatterjee and Scotese, 2010; Chatterjee et al., 2017) have all been invoked as stepping stones for faunal exchange. The subaerial nature and extent of some of these features has been questioned or refuted (Ali and Aitchison, 2008; Ali and Krause, 2011; Smith et al., 2016; Kapur and Khosla, 2016; Hu et al., 2016). Nonetheless, these bio-connection hypotheses provided explanations for the observation that the ‘mixed’ fauna of the Indian subcontinent, including taxa closely related to those in both Gondwanan and Laurasian landmasses, has persisted since its isolation in the Late Cretaceous and Paleocene (Sahni et al., 1987; Prasad and Sahni, 2009; Chatterjee and Scotese, 2010; Smith et al., 2016; Chatterjee et al., 2017).

Comment [TH1]: R2a

[PLACE FIGURE 1 ABOUT HERE, 2 COLUMNS]

The major Late Cretaceous vertebrate fossil sites of the Indian subcontinent are located in the Deccan Volcanic Province (DVP) of central and western India, the Cauvery Basin of southeastern India, and the Narmada Valley of Central India (see reviews in Prasad, 2012; Kapur and Khosla, 2016). Within these areas, the major fossiliferous vertebrate-bearing strata include the Bagh beds of the Narmada Valley, the Lameta Formation and the intertrappean beds of the DVP, and the Kallamedu Formation in the Cauvery Basin. All four are dominated by vertebrate microfossils, but fragmentary and fragile larger bones are also represented. Previous work has confirmed that the Lameta and intertrappean beds are extremely similar to one another faunally. The fauna of the Kallamedu Formation, however, more closely resembles that of the Maevarano Formation of Madagascar (Halliday et al. 2017), on the

basis of the preservation of taxa such as a *Simosuchus*-like notosuchian crocodyliform (Prasad et al., 2013; Prasad and Goswami, 2015), which appears to be absent from the DVP. Other classically ‘pan-Gondwanan’ taxa such as titanosaurian and abelisaurid dinosaurs, bothremydid turtles, and gondwanatherian mammals are found across the Late Cretaceous of the Indian subcontinent, as well as “madtsoiid” snakes (Bonaparte, 1999). This last group is known from the Cretaceous and Paleocene of Gondwana, but it is worth mentioning that the identification of some specimens to Madtsoiidae should be treated with caution (Rio and Mannion, 2017). Both the DVP and the Kallamedu Formation also contain taxa generally associated with Laurasia, such as a possible troodontid dinosaur (Goswami et al., 2013), phyllodontid fish (Halliday et al. 2016), pelobatid frogs (Sahni et al., 1982), alytid (=‘discoglossid’) frogs (although referral of Indian specimens to these families is doubted by Agnolin, 2012) and anguimorph lizards (Prasad and Rage, 1991; 1995; 2004) and eutherian mammals (Prasad et al., 1994; Rana and Wilson, 2003; Prasad et al., 2010; Goswami et al., 2011). In addition to the DVP and the Kallamedu Formation, the shallow marine Karai Formation of the Cauvery Basin primarily records marine invertebrates, but shark and ichthyosaur remains are also known (Underwood et al., 2011). Only shark and dinosaur teeth have so far been recovered from the Upper Cretaceous Bagh Group of the Narmada Valley (Prasad et al., 2016; Prasad et al., 2017). Finally, the Pab Formation of Pakistan represents a terrestrial Late Cretaceous ecosystem, also from the Maastrichtian, and is characterized by a dinosaur fauna dominated by titanosaurs, as well as the baurusuchid crocodyliform *Pabwehshi* (Wilson et al., 2001; Wilson et al., 2005).

Comment [TH2]: R3a

Comment [TH3]: R3b

[PLACE FIGURE 2 ABOUT HERE, 2 COLUMNS]

The most productive vertebrate-bearing Paleocene formation of the Indian subcontinent is the nearshore Fatehgarh Formation, which lies in the Barmer Basin of northwestern India (Rana et al., 2006b). The vertebrate fauna recovered from this basin was considered to be of Late

Cretaceous age (Mathur et al., 2006), but this estimate has been revised to the Early Paleocene on the basis of vertebrate faunal differences with the Deccan intertrappean beds (Rana et al., 2006b). Recently, a yet-to-be-described chondrichthyan fauna has been recovered from the shallow marine Lower Paleocene Niniyur Formation of the Cauvery Basin, indicating close shallow marine connections between India and northwestern Africa and southern Europe (Prasad pers. obs.), but this has not been included in the present study. In addition, the Danian Khadro Formation of Pakistan has yielded probable madtsoiid snake and dyrosaurid **crocodylomorph** material (Storrs, 1986; Rage et al., 2014), while the Late Paleocene-Eocene Akli Formation of the Barmer Basin preserves a diverse fish fauna (Rana et al., 2005).

**Comment [TH4]:** R2b, R3c

In addition, some Deccan intertrappean beds have been proposed to be Early Paleocene (Wilson et al., 2016), but these are disputed and are not included in the present analysis. Fossil sites from the Early Eocene of the Indian subcontinent are concentrated in shallow marine lignite deposits, and many specimens have been recovered from the associated mines at Vastan and Tadkeshwar (the Cambay Shale Formation) and Panandhro (the Naredi Formation). The Cambay Shale includes several large “ungulate” taxa including endemic Indian forms, such as cambaytheres and anthracobunids, and more cosmopolitan families such as palaeoryctids, nyctitheriids, hyaenodontids, notharctids, and leporids, to name but a few (see review of Indian subcontinental early Eocene vertebrates in Chatterjee et al., 2017). The Panandhro lignite mine fauna is dominated by cosmopolitan fish taxa, such as lepisosteids and many chondrichthyans. A taxonomically diverse fish fauna has also been described from the marginal marine to shallow marine deposits associated with lignite seams of the Lower Eocene Akli and Kapurdi formations of the Barmer Basin (Rana et al., 2005; Rana et al., 2006a), and the Khuiala Formation of the Jaisalmer Basin (Kumar et al., 2007) in

western India. In the north of India and in Pakistan, the shallow marine Subathu and Kuldana Formations contain some of the earliest cetaceans (Sahni et al., 1981; Kumar and Sahni, 1985; Thewissen et al., 2001; Thewissen et al., 2007), distinguishing them from the sites in central and western India. Finally, the Mami Khel and Ghazij localities of Pakistan contain several mammalian groups such as dichobunid artiodactyls, chalicotheres, and early primates and carnivorans (e.g., Clyde et al., 2003; Missiaen and Gingerich, 2012; 2014).

[PLACE FIGURE 3 ABOUT HERE, 2 COLUMNS]

Middle Eocene sites include the aforementioned Subathu and Kuldana sites, as well as the marine Harudi Formation of Kachchh, which, like the Subathu and Kuldana formations, is dominated by protocetid and remingtonocetid whales, and the Chorgali Formation, from which helaletid and raoellid artiodactyls are known (Thewissen et al., 2001).

Assessing the degree to which transoceanic or island-hopping dispersal during the Indian subcontinent's isolation affected overall composition of its terrestrial and freshwater vertebrate fauna is an important aspect of its paleobiogeographic reconstruction. Several qualitative comparisons have been made between the Indian subcontinent and other landmasses during the Late Cretaceous and later, but few quantitative comparisons exist. Faunal similarity metrics allow quantification of the degree to which sites, formations, or other geographic/geologic divisions share taxa, and have a long history in paleontology from the identification of local ecological differences (e.g., Raup and Crick, 1979) to the formation of barriers to migration over geological time (e.g., Cecca, 2002). Networks are useful ways of mathematically displaying the presence or absence of relationships among objects. Combining the two to determine the Indian subcontinent's close faunal relations during its long period of isolation will help to quantify and potentially clarify previously described patterns.

When describing a biota as ‘cosmopolitan’, ‘endemic’, or using the presence of shared animals or plants to infer general biogeographic relationships, it is important to consider the biota as a whole, and to integrate information from elsewhere. Doing so allows for further testing of important paleobiogeographic scenarios and questions. For instance, in the case under consideration here, does the presence of Laurasian clades in the Late Cretaceous of the Indian subcontinent cause it to be faunally intermediate with respect to the southern and northern continents? Does immigration from Laurasia explain the observed relative lack of similarity between the sites of the DVP on the one hand and both the Cauvery Basin and Madagascar on the other? To answer these and other questions, it is necessary to compare simultaneously the faunal composition of Late Cretaceous and Early Paleogene vertebrate-bearing localities worldwide.

## METHODS

### **Faunal Similarity Networks**

Networks are an informative way of displaying and analysing the interaction between different pools of data, and have a long and successful history of use in, for example, the social sciences, in which entire journals are dedicated to network models, and epidemiology (e.g., Reis et al., 2007). Networks have been used in evolutionary biology in the context of modularity (Esteve-Altava et al., 2015) and ecology (Blonder et al., 2012), while their mathematical similarity to unrooted phylogenetic trees and cluster hierarchies (both of which are merely special cases of a network graph) has allowed them to be used to address macroevolutionary questions concerning phylogenetic relationships (Baptiste et al., 2013) and paleobiogeography (Kiel, 2017; Dunhill et al., 2016). Network methods allow the testing of wider ranges of hypotheses than bifurcating hierarchical clustering methods in

Comment [TH5]: R2c



paleobiogeography, or bifurcating cladograms in phylogenetic inference. Uncertainty in relationships or similarity can be incorporated into the network, permitting a more nuanced picture of macroevolution to be obtained. In the context of paleobiogeography, use of networks can investigate the degree to which clustering of faunas is based on geography or environment, as has been done by Kiel (2017) on Tethyan brachiopod faunas. More promising, however, is the capability to assess how ecosystems change over time with respect to other sites. Sidor et al. (2013) used an adapted version of the network edge density statistic to compare the homogeneity of terrestrial faunas across the Permo-Triassic boundary. Changes in the values of such network parameters may be able to indicate the growing or waning importance of certain critical faunas, chart the movements of continents, or demonstrate changing global ecosystem dynamics over important geological intervals such as mass extinction events. A modification of this method correcting for phylogeny was introduced by Button et al. (2017) to do exactly that: identify a higher level of cosmopolitanism in the aftermath of the Permo-Triassic mass extinction. Here, it is worth noting that the networks of Sidor et al. (2013) and Button et al. (2017) are structurally different from those of Kiel (2017). Sidor et al. (2013) represents both taxa and localities as different classes of node, with edges connecting a taxon to a locality if that taxon is represented in that locality. On the other hand, Kiel (2017) treats only localities as nodes, with edges connecting localities with weights proportional to some faunal similarity metric. It is this latter approach that we use here.

### **Global Patterns**

Three network statistics are of potential use when describing the relationships among global faunas. The first is the density statistic, which measures the proportion of all possible edges between nodes that are observed. A network with density of one is ‘complete’, and has all

nodes connected to all other nodes. A network with density of zero has no edges at all. In the context of a faunal similarity network, a complete network would represent a set of localities, all of which have pairwise similarity scores above the threshold value. Depending on the scale of the analysis, this could be interpreted as evidence that multiple sites are part of the same local ecosystem, or evidence for widespread cosmopolitanism across many taxa. Conversely, a network with no edges would show that all sites are independent from one another, indicating a high degree of endemism, and implying long periods of isolation.

Secondly, node centrality is a family of statistics used to identify highly connected nodes. Betweenness centrality takes the shortest paths between all pairs of nodes, and calculates the number of times those paths include any given node. In the context of faunal similarity indices, a node with a high betweenness centrality would represent a true ‘mixed’ fauna comprising several taxa that are otherwise representative of two or more clusters of localities.

The final network statistic considered here is network modularity. Clusters of nodes that are more linked to one another than to external nodes can be identified using the betweenness statistic as applied to edges rather than nodes. The modularity statistic of a matrix, given the identified clusters, quantifies the degree to which those clusters are truly separate modules.

Here, we employ all three statistics to document the changing position of the Indian subcontinent in a global paleobiogeographic context from the Late Cretaceous through to the Eocene.

## **Data Collection**

Global terrestrial, freshwater, and shallow marine occurrence data for vertebrate families and genera were downloaded from the Paleobiology Database ([paleobiodb.org](http://paleobiodb.org), access date 6<sup>th</sup> of June, 2017), spanning all time periods from the Late Cretaceous to the Eocene inclusive. These were then vetted by correcting spellings, merging duplicate names, removing

ichnotaxa and ootaxa, ensuring that the familial assignment of each genus was correct, and that formation names were consistent and had complete faunal occurrence lists. The modified Paleobiology Database files are found in Appendix 1. Occurrences were divided into 33 time bins defined by uncertainties in fossil range dates, and were analysed both as separate time bins and as a whole (Table 1). Within each analysis, formations with fewer than three families or genera present were excluded. Family- and genus-level data were analysed separately; for the purposes of this paper, all graphs presented and discussed use the family-level dataset unless otherwise stated. Genus-level data and results can be found in Appendix 1, but because families are more inclusive, discussion of faunal similarity patterns are more fruitful at that level. Pairwise faunal similarity measures were calculated using the modified Forbes metric (Alroy, 2015a), which ranges from zero if no taxa are shared between two sites to one if they are identical, or if one fauna is a subset of the other. The primary advantage of the modified Forbes metric is that it is robust to uneven and biased sampling (Alroy, 2015b), a well-known problem in paleontological datasets.

[PLACE TABLE 1 ABOUT HERE]

An additional advantage over other methods is that it does not require the data to include numbers of specimens, merely coding a taxon as present or absent in each locality. Thresholds in Forbes metric scores varying from 0.05 to 0.95 were applied to each analysis, in each case treating all values less than the threshold as zero. Undirected weighted graphs were drawn using the *igraph* (Csardi and Nepusz, 2006) package in R (R Development Core Team, 2010), using formations as nodes and non-zero Forbes scores as edges. Without thresholding the network at all, the network is invariably extremely dense to the point of being uninformative. Thresholds gradually remove those less connected faunas, leaving only those with some degree of connectivity in the graph. Threshold values in the discussion are typically 0.5 (when the presence of an edge indicates greater similarity than dissimilarity),

except when otherwise stated. Nodes were identified that connected to formations on the Indian subcontinent after appropriate thresholds were determined. Clusters were identified using the edge betweenness statistic, and the modularity of the thresholded network calculated based on these clusters. Network edge density was calculated in each time-binned analysis and at each threshold level, to give a measure of ‘decay’ of density in a given time bin. Betweenness metrics of centrality were compared for localities in different continents. The full R code for this analysis, including Alroy’s Forbes functions, are found in Appendix 2.

[PLACE FIGURE 4 ABOUT HERE, 1 COLUMN]

Network density, a measure of the total proportion of the possible edges, is a way of measuring homogeneity among faunas. Dense networks or subnetworks contain a greater proportion of taxa that are found in all or most faunas. For example, a network density of one without thresholding would indicate that all sites shared at least one taxon with all other sites, suggesting a strong degree of connectivity among the ecosystems. Conversely, a network density of 0 would indicate that all faunas were exclusively composed of endemic taxa (Figure 4).

Comment [TH6]: R2d

## RESULTS AND DISCUSSION

### The Late Cretaceous of the Indian subcontinent

Four Late Cretaceous (Bin 13, see Table 1) formations from subcontinental India are represented by sufficient taxa to be included in the analysis: the Kallamedu Formation of the Cauvery Basin, the Lameta Formation and the intertrappean beds – all from India – and the Pab Formation of western Pakistan. In the Late Maastrichtian, at a threshold of 0.75, the Kallamedu Formation has connections to the Madagascan Maevarano (0.84) and Colombian Ortega (0.76) formations. The Ortega Formation has yielded few fossils, and here is

Comment [TH7]: R2e

represented by only three families, but the similarity between the Kallamedu and Maevarano formations is based on substantial faunal overlap of a large sample size. The Lameta and intertrappean beds are connected (0.86), but are not similar to any other locality at this threshold, while the Pab Formation is isolated, though most similar to the Kallamedu Formation (0.64). No Indian site shows high similarity scores with any African site, but at a wider level, Gondwanan sites, including those from Africa and Australia, cluster together, indicating a strong level of cohesion of a “pan-Gondwanan” fauna throughout the Cretaceous.

Comment [TH8]: R2f

### **The Paleocene of the Indian subcontinent**

The Indian early Paleocene (Bin 14, see Table 1) vertebrate fossil record is essentially blank, with the possible exception of a few of the later intertrappean beds, which are thought by some to represent a post-Cretaceous ecosystem (Singh and Kar, 2002; Keller et al., 2009; Wilson et al., 2016), as well as the Fatehgarh, Akli, and Khadro formations. The Fatehgarh Formation is entirely represented by fish, and has no connections with any other Early Paleocene formation at a threshold of 0.5. The Akli Formation is most similar to the Aruma Formation of Saudi Arabia (0.54), but otherwise has no similarity to any other Late Paleocene fauna at a threshold of 0.5. The Khadro Formation has only yielded a madtsoiid snake and a dyrosaurid crocodylomorph among its vertebrate remains, and as such has too few taxa to be included in this analysis.

Comment [TH9]: R2g, R3d

### **The Eocene of the Indian subcontinent**

By the Early Eocene (Bin 25, see Table 1), the overall signal demonstrating a Gondwanan heritage is gone in all Indian localities. At a threshold level of 0.6, the Cambay Shale is most similar to the European Ypresian (European Reference Level MP 8-9) localities at Sézanne-Broyes (France) and La Coma (Spain), as well as the Kuldana Formation of Pakistan and the

Niushan Formation of China. The Mami Khel Formation has connections with the Suffolk Pebble Beds (UK), the Willwood Formation (USA), and the Ghazij Formation (Pakistan), which is in turn connected to the Ypresian Gres d'Assignan locality in France. The Subathu Formation, which ranges from the Late Paleocene to the Middle Eocene, is unconnected to any other locality throughout the Early Eocene. The fish fauna of the Kapurdi Formation clusters with two other major fish dominated faunas, those of Monte Bolca in Italy, and Tallahatta, USA.

In the Middle Eocene (Bin 30, see Table 1), the patterns are not qualitatively different from those of the Early Eocene. The Subathu, Kuldana, and Chorgali formations of the Indian subcontinent are all similar to one another, with the Subathu and Kuldana formations displaying some similarity with the Irtysh River Formation of China, and the Kuldana Formation similar to the Grabels Locality (MP 13-14) of France. Separated from these are the Naredi Formation, which displays similarity with the Yegua and Shark River formations of North America, and the Elmore Formation of the UK. The only Gondwanan connection exists between the Harudi Formation of India and the Mokattam Formation of Egypt. This African connection is entirely due to both sites being shallow marine formations dominated by marine mammals – both protocetids and sirenians. Eocene sites of the Indian subcontinent were less similar to one another than they had been in the Cretaceous, and were dominated by Laurasian taxa, with the signal particularly coming from various families of euungulates (the group comprising artiodactyls, perissodactyls, and their stem relatives). The lack of similarity to one another is perhaps driven by a greater environmental heterogeneity. Whereas the sampled Late Cretaceous sites of the Indian subcontinent are mostly fluviolacustrine sites dominated by terrestrial taxa, the Early to Middle Eocene includes both terrestrial and shallow marine localities.

More broadly, Eocene Gondwanan localities are no longer as closely associated with one another as they were in the Cretaceous, with the exception of a cluster of South American sites that preserve their unique endemic identity. The switch from Cretaceous to Paleogene faunas has coincided with the loss of a unique Gondwanan identity, and greater similarities between north and south.

The Laurasian signal throughout the Eocene of India reflects shared members of families and genera but, at a more qualitative level, comparisons among the families reveal that this Laurasian affinity in terms of euungulates is part of a bigger story concerning globally distributed and closely related lineages. The one truly endemic family of euungulates in the Eocene of the Indian subcontinent is the cambaytheres, thought to be most closely related to perissodactyls (Cooper et al., 2014; Rose et al., 2014). This has led some to suggest that perissodactyls originated on the Indian subcontinent, but the plethora of other lineages also considered to be close relatives of perissodactyls, such as the North American phenacodontids (Halliday et al., 2015), the Asian phenacolophids (Mao et al., 2016), and the South American litopterns and notoungulates (Welker et al., 2015; Westbury et al., 2017) imply that these various groups may be closely related to one another, and a Paleogene global distribution may be in effect. A modification made to the aforementioned alternative network approach to biogeography (Sidor et al., 2013), which incorporates phylogenetic distance (Button et al., 2017), might be applicable to the faunal similarity approach of Kiel (2017), thereby allowing different biogeographic hypotheses to be tested in a phylogenetic framework.

### **Global faunal network of the Cretaceous and Paleogene**

Globally, and without dividing the data into time bins, faunal clustering at a threshold level of 0.75 initially revealed an unsurprising split between the Cretaceous and Paleogene faunas. Within each era-level cluster, faunas were broadly divided into geographic bins. In the Cretaceous, Gondwanan localities were tightly clustered together, with all Indian sites – namely the intertrappean beds, Lameta Formation, and the Kallamedu Formation – clustered together to the exclusion of other sites. At a threshold level of 0.75 (Figure 5), the Kallamedu Formation was linked to the Maevarano Formation of Madagascar and the Ortega Formation of Colombia (Ezcurra, 2009). It must be noted that the Ortega Formation contains only very fragmentary fossils that cannot be identified below family level (Ezcurra, 2009), while only minimally meeting the sample size standard for inclusion in this analysis. In addition, the assignment of the dinosaur remains to the Ortega Formation has been disputed (Jiménez-Velandia, 2017). For the purposes of this analysis, as the fossils included here were collected from the same place, the label assigned to that group does not matter, but the small sample size must qualify interpretation of this locality as being closely faunally associated. Comparisons involving smaller numbers of taxa are far more susceptible to change on the discovery of additional material. In addition to the Maevarano and Ortega formations, similarity was found between the Kallamedu Formation and the Rognacian sites of France (Tabuce et al., 2004; Tortosa et al., 2014), on the basis of several otherwise Gondwanan lineages such as abelisaurids, lepisosteids, and bothremydids. Another group contributing to this similarity are titanosaurs, which are most abundant in Gondwana but do have a substantial Laurasian component throughout the Cretaceous. All four sites are Maastrichtian in age. The Cretaceous intertrappean beds and Lameta Formation, and the Paleocene Fatehgarh Formation clustered with one another and with the Cerrejón Formation of Colombia, demonstrating again the close faunal similarities among the Gondwanan continents during the Mesozoic. Close similarities in Late Cretaceous faunas of South America, Madagascar, and

**Comment [TH10]:** R2h



India to the exclusion of Africa may represent vicariance, supporting the Africa-first hypothesis (Krause et al., 2006). However, many have argued for later dispersals between the Indian subcontinent, Madagascar, Africa and southern Europe close to the Cretaceous-Paleogene boundary, as exemplified by madtsoiid snakes, majungasaurine abelisaurids, and adapisoriculid mammals (Prasad et al., 2010; Tortosa et al., 2014; Rio and Mannion, 2017).

[PLACE FIGURE 5 ABOUT HERE, 2 COLUMNS]

Eocene Gondwanan sites in general, and those from the Indian subcontinent specifically, are more separated, and all are closely connected with Laurasian localities, or entirely separated from the main cluster (Figure 5). Among the former Gondwanan continents in the Cenozoic, it is only South America for which geography is a bigger driver of global faunal affinities than time, with all localities from that continent found as a separate cluster. Whereas clustering in the Cretaceous was driven by geography, with several close connections between temporally divergent localities spanning approximately 30 million years, the Paleogene sites across the same period are divided into at least three major temporal groups – the Paleocene as a whole, the Early Eocene, and the Middle Eocene. In each temporal group, the abundant North American sites provide the backbone to the network, with connections forward and backward in time, with Asian and European sites connecting to that network in temporally defined clusters. Indian localities such as the Naredi Formation and the Cambay Shale are often part of these offshoots, variously close to Laurasian localities or isolated as an unconnected fauna.

When time bins were considered separately, the Maastrichtian global sites showed a very similar pattern to all sites taken at once (Figure 6). The Kallamedu Formation of India was highly connected at a threshold level of 0.75, connecting to the Maevarano Formation of Madagascar, the Pab Formation of Pakistan, and the DVP faunas of India, and both South

American and European sites. Europe, for the most part, clusters with Gondwana, recapitulating the Late Cretaceous Eurogondwana concept of Le Loeuff (1991; see also Gheerbrant and Rage, 2006; Rabi and Sebők, 2015; Rio and Mannion, 2017; Ezcurra and Agnolin, 2012), while North America and Asia are divided into three major clusters – the southeastern US, a combined East Asia and Western Interior USA cluster, and a China-Mongolia cluster.

Comment [TH11]: R2j

[PLACE FIGURE 6 ABOUT HERE, 1 COLUMN (2 IF NECESSARY)]

In the early Eocene, at a threshold of 0.75, South America and Africa are resolved as fully unconnected clusters, while the Indian subcontinent is part of a major grouping including all North American, European, and approximately half of the Asian localities (Figure 7), demonstrating strong Laurasian affinities during this time. The closest connections for the Cambay Shale and Subathu formations are through the Niushan Formation of China and the Sézanne-Broyes locality (MP 8-9) in France, which in turn connect more widely to Europe and Asia. This pattern is maintained through to the Late Eocene, during which time the faunas of the Indian subcontinent maintain connections with northern rather than southern landmasses (Figure 8).

[PLACE FIGURE 7 ABOUT HERE, 1 COLUMN (2 IF NECESSARY)]

[PLACE FIGURE 8 ABOUT HERE, 1 COLUMN (2 IF NECESSARY)]

### **Density, Centrality, and Modularity**

Throughout the time period covered by this analysis, edge density of time-binned global networks at the family level remained high (between 0.15 and 0.6), while edge density at the genus level was low during the Cretaceous and high in the aftermath of the end-Cretaceous mass extinction and for the duration of the Paleocene. Previous observations of the end-

Permian mass extinction have suggested a global disaster fauna (Sahney and Benton, 2008; Button et al., 2017; although this was not found in the network analysis of Sidor et al., 2013), and as such, we might have expected an increase in network density through the Cretaceous dataset. The increase in density observed at the global scale is probably due to a high proportion of Paleocene sites from the Western Interior of North America. With geographically connected and proximate sites, it is expected that some overlap in fauna – and therefore an edge in the network – would be more likely. When a comparison is made at solely the continental level, there is no difference in the edge density between the Late Cretaceous and Early Paleocene of North America, suggesting that the apparent global increase is probably a result of spatial bias of fossil localities rather than a result of any identifiable changes in patterns of global faunal heterogeneity. The differences in the geographic arrangements of the continents during these two mass extinction events make any direct comparison difficult – reduced migration as a result of oceanic barriers in the Late Cretaceous perhaps making faunal cosmopolitanism more difficult than on Pangaea at the Permo-Triassic boundary.

[PLACE TABLE 2 ABOUT HERE]

Betweenness centrality scored at threshold 0.5 revealed that, in the Late Cretaceous, the Kallamedu Formation had amongst the highest betweenness scores in both Bins 12 and 13, being the sixth most central in the late Maastrichtian as part of 144 of a possible 2,301 shortest paths. The Lameta Formation also had relatively high centrality scores. For the majority of the Eocene, no site on the Indian subcontinent was among the most central localities, but had consistently low, non-zero scores (Table 2). The one exception to this pattern is the fauna of the Kuldana Formation for which the error bars extend into Bin 33. Here, the Kuldana Formation acts as a bridge between two large clusters, and thus is part of nearly half of all shortest paths. This high score is not, however, a result of a mixed

Gondwanan and Laurasian fauna, but is instead a result of anthracobunid, diacodexid, and omomyid placental mammals. Further, the non-zero scores exhibited by other Cenozoic Indian subcontinent faunas are largely a result of the connection among shallow marine sites rather than a mixed terrestrial fauna. The overall pattern of higher scores in the Late Cretaceous followed by generally lower scores through the Paleogene suggests that the Late Cretaceous vertebrate fauna of the Indian subcontinent can reasonably be said to be a particularly highly ‘cosmopolitan’ fauna with a mixture of northern and southern clades, linking together sites from Gondwana and Laurasia. The Eocene of the Indian subcontinent, on the other hand, while it contains a number of clades with Gondwanan affinities, is dominated by an influx of Laurasian clades, particularly placental mammals. The Gondwanan component to the Eocene faunas is reduced to being relictual, with little impact on placement in a faunal similarity network.

#### **A theoretical Paleocene fauna from the Indian subcontinent**

Comment [TH12]: R3e

Although the scarcity of Paleocene rocks from the Indian subcontinent means that its Paleocene fauna may never be well known, the occurrences of taxa in both the Cretaceous and Eocene of the subcontinent is indicative of at least some of the faunal components during this missing interval. Of the 42 families present in the Maastrichtian of the Indian subcontinent, 11 are also found in the Eocene. Some of these are known from those few Paleocene sites in continental India to have yielded vertebrate fossils, such as dyrosaurid crocodylomorphs (Storrs, 1986; Prasad and Singh, 1991; Rana and Sati, 2000; Khosla et al., 2009; Smith et al., 2016) and madtsoiid snakes (Rage et al., 2014). Myliobatid, pycnodont, and eotrigonodontid fish are known from the Cretaceous, Eocene, and also the early Paleocene Fatehgarh Formation (Kumar and Loyal, 1987; Rana, 1990; Rana et al., 2006b; Smith et al., 2016). In addition to these taxa, there are six families known from Cretaceous

and Eocene sites in the Indian subcontinent but absent from the Paleocene, namely ariid (Jain and Sahni, 1983; Bajpai and Thewissen, 2002) and phyllodontid fish (Rana et al., 2004; Halliday et al., 2016), boid snakes (Jain, 1989; Wilkson et al., 2010; Smith et al., 2016), crocodylids (Rana and Sati, 2000; Bajpai and Thewissen, 2002), alytid frogs (Prasad and Rage, 1991; Bajpai et al., 2005), and adapisoriculid mammals (Prasad et al., 2010; Goswami et al., 2011; Kapur et al., 2017). When combined with known vertebrate occurrences from the Paleocene faunas of the Fatehgarh, Akli, and Khadro formations, the inhabitants of a hypothetical Paleocene Indian subcontinent can be placed into the faunal network. This is, of course, extremely speculative: there is the assumption that presence in the Cretaceous and Eocene necessitates presence in the Paleocene, which might not be the case, and the lack of sampling is necessarily restrictive. Nonetheless, theorizing on the composition of otherwise absent faunas allows us to explore possibilities while also producing hypotheses that could be confirmed or rejected by future discoveries.

Here, the ‘Theoretical Paleocene Fauna’ (TPF) of the Indian subcontinent occupies a place in the network distinct from the majority of North American sites. Largely due to the presence of dyrosaurids, the early Paleocene is strongly similar to the Umm Himar Formation of Saudi Arabia. High similarity scores between TPF and the Umm Himar Formation are partially a result of the low diversity of the latter. Dyrosaurids are also known from the Paleocene phosphate basins of Morocco (Jouve et al., 2005), but other differences between those faunas and TPF result in lower similarity scores. TPF also has some similarity to the fish-dominated marine Hornerstown Formation in New Jersey, USA, as well as the Santa Lucia Formation of Bolivia, which has also yielded both boid and madtsoiid snakes. If included with middle Paleocene localities, TPF shows affinities with the Cerrejón Formation (Colombia) and the Jbel Guersif Formation (Adrar Mgorn localities, Thanetian of Morocco), while Late

Paleocene sites that cluster with TPF include the Aruma and Itaborai formations, as well as the ‘Argiles à Lignites du Soissonais’ fauna (MP 7, Early Eocene of Rivecourt) in France. As only those taxa present in the Cretaceous and earliest Paleocene are considered for this ersatz Paleocene fauna, it is unsurprising that the majority of high faunal similarities are between localities on the Indian subcontinent and elsewhere in Gondwana. Given, however, that these are taxa that are also present in the Eocene, and which in the Eocene also cluster with Gondwanan sites, this demonstrates the extent to which immigration must be generating the observed similarities between Eocene faunas of the Indian subcontinent and Laurasia.

We found no relationship between familial faunal similarity and distance between latitude-longitudinal sites, contrary to the hypothesis that greater distance would result in lower faunal similarity. The exception to this is during the Paleocene, when the relationship is strong ( $R^2$  of 0.5 or more). This pattern remains true even when looking solely at North America,

**Comment [TH13]:** R1c

indicating that oceanic barriers are not the cause, and that there is something fundamentally different about the Paleocene data that results in a different pattern. Although a full exploration of this pattern is beyond the scope of this paper, it may be that Paleocene families are typically younger following radiation, and having had less time to disperse, are more likely to have a distance-controlled distribution. Alternatively, the lack of substantial high-latitude dispersal during the Paleocene compared with both the Cretaceous and Eocene (e.g. Beard and Dawson, 1999; Martin et al., 2005; Hooker, 2015) might have resulted in a reduction in the homogenizing effect of intercontinental migration. Linnaean ranks are arbitrary, and therefore families need not be equivalent among different clades, even where defined. Indeed, this is known to be the case among extant organisms (Avise and Liu, 2011).

**Comment [TH14]:** R1d – Hard to disentangle. Compare clade age with distribution of ages of families included in each bin. Are Paleocene clades fundamentally different from those in the Cretaceous and Eocene. If not to do with proliferation of young families controlled by distance, are they clustered by environment?

Families are defined solely by morphological differences greater than that of a genus and are a hypothesis of relatedness, but in rapid radiations such as those thought to have occurred in

mammals, teleosts, and birds after the end-Cretaceous mass extinction, rates of morphological evolution are expected to have increased substantially (Beck and Lee, 2014; Halliday et al., in review), so ranks in different time periods might not be equivalent. The arbitrariness of Linnaean ranks may also impact the study in differential treatment of taxonomy by different workers. The family concept is little-used among dinosaur workers (Richard Butler, pers. comm.), but remains important for distinguishing mammals, where the enigmatic “condylarths” can reliably be divided into more-or-less monophyletic groups (but see De Bast and Smith, 2013 for a counterexample) that are defined as families, but whose higher-level relationships are unclear (Halliday et al., 2015). Even with perfect vetting of the data, different practices in the definition of arbitrary taxonomic ranks among paleontologists can impact later interpretation (see Hendricks et al., 2014 for related discussion about non-species ranks in the fossil record). Although ranks are arbitrary, the analyses within each time bin will be largely unaffected. The equivalence of the unit of measurement of ‘family’ is irrelevant to the calculated similarity, where each example of that unit is defined equivalently throughout the bin. It is in comparing network statistics between time bins that we might have reason for concern, but the pattern exhibited by abelisaurids leads us to have confidence that the Late Cretaceous networks are not substantially different from the Cenozoic networks as a result of substantially different data; the clustering of abelisaur-bearing faunas of a Madagascar-Indian subcontinent cluster close to Southern Europe mirrors phylogenetic hypotheses about these taxa, resulting in plausible biogeographic scenarios.

Comment [TH15]: R1b

## CONCLUSIONS

As has long been known, the faunal composition of Late Cretaceous and Paleogene sites on the Indian subcontinent is a mixture of taxa with Gondwanan and Laurasian affinities. Faunal network analysis demonstrates that the faunal signal from the Cauvery Basin, the Pab

Formation, and the Deccan Volcanic Province links these Indian faunas most strongly with South American and Madagascan localities, both in pairwise comparisons of faunal similarity and clusters derived from edge betweenness statistics. In these clusters, the Kallamedu Formation falls with the Maevarano Formation of Madagascar, as in previous work, but also with several South American sites in particular – the Ortega Formation, but at lower threshold values, also the Marília and Adamantina Formations, while the sites of the DVP cluster separately. Those few clades present in the Cretaceous of the Indian subcontinent with Laurasian affinities – for instance, alytids, troodontids, phyllodontids, and adapisoriculids – are exceptions to the rule, but are numerous enough to result in the Kallamedu Formation in particular being one of the most faunally connected localities of the Late Cretaceous under the node betweenness statistic.

The Paleocene vertebrate fauna of the Indian subcontinent is poorly known, but those clades that persisted from the Late Cretaceous through the Paleocene and into the Eocene retained their historic ties with Gondwana, even while the signal as a whole shifts in the Eocene to one favouring a Laurasian-dominated fauna, relegating those pan-Gondwanan clades to relictual status within a larger ecosystem. The Laurasian signal is largely driven by shared placental mammalian families that have widespread Laurasian distributions. These similarities reflect significant dispersal events that took place in the early Paleogene among the Indian subcontinent, Asia, Europe, and North America (Krause and Maas, 1990; Beard and Dawson, 1999; Bossuyt and Milinkovitch, 2001; Bowen et al., 2002; Clyde et al., 2003; Smith et al., 2006; Clementz et al., 2011). The subsequent evolution and extinction of clades elsewhere weakened the faunal similarity with other Gondwanan landmasses, and as a result, the Eocene faunas of the Indian subcontinent have lower centrality scores. This metric reflects the lessening degree to which the subcontinent's faunas can be said to be a mixed,



cosmopolitan fauna as the Cenozoic progresses, highlighting the importance of intercontinental migration in the development of faunas, and emphasising the biogeographic uniqueness of the diverse fauna on the Indian subcontinent at the end of the Mesozoic.

#### AUTHOR CONTRIBUTIONS

TJDH and AG designed the analysis, TJDH wrote the code and conducted the analysis, and all authors screened segments of the data and contributed to the manuscript.

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## TABLES



Table 1 - Time bins into which the data set was divided. Divisions between bins encompass the uncertainties in fossil dating. Fossil occurrences were placed into every bin in which they may have occurred. This approach ensures that faunas with non-overlapping date ranges are not erroneously placed in the same bin for analysis, while allowing flexibility in the sets of faunas compared. Differences in bin duration are not problematic in the context of this analysis as the patterns discussed in this analysis are not sample-size dependent. Bins in bold are those discussed in the manuscript as Late Cretaceous, Early Paleocene, Early Eocene, and Middle Eocene respectively.

<i>Bin</i>	<b>Maximum age</b>	<b>Minimum age</b>	<b>Description</b>
1	-	100.5	Earlier than analysis
2	100.5	99.6	Earliest Cenomanian
3	99.6	93.9	Cenomanian
4	93.9	93.5	Earliest Turonian
5	93.5	89.8	Turonian
6	89.8	89.3	Earliest Coniacian
7	89.3	86.3	Coniacian
8	86.3	85.8	Early Santonian
9	85.8	83.6	Late Santonian
10	83.6	83.5	Earliest Campanian
11	83.5	72.1	Campanian
12	72.1	70.6	Early Maastrichtian
<b>13</b>	<b>70.6</b>	<b>66</b>	<b>Maastrichtian/Lancian</b>
<b>14</b>	<b>66</b>	<b>63.3</b>	<b>Danian/Puercan</b>
15	63.3	62.5	Danian/Torrejonian

16	62.5	61.7	Danian/Torrejonian/Peligran
17	61.7	61.6	Danian/Tiffanian
18	61.6	59.2	Selandian/Tiffanian
19	59.2	59	Thanetian/Tiffanian
20	59	58.7	Thanetian/Tiffanian/Itaboraian
21	58.7	57	Thanetian/Tiffanian/Itaboraian/Gashatan
22	57	56.8	Thanetian/Tiffanian/Riochican/Gashatan
23	56.8	56	Thanetian/Clarkforkian
24	56	55.8	Ypresian/Clarkforkian
<b>25</b>	<b>55.8</b>	<b>50.3</b>	<b>Ypresian/Wasatchian</b>
26	50.3	48.6	Ypresian/Bridgerian
27	48.6	48	Ypresian/Arshantan/Sharamurunion
28	48	47.8	Ypresian/Mustersan
29	47.8	46.2	Lutetian/Bridgerian
<b>30</b>	<b>46.2</b>	<b>41.3</b>	<b>Lutetian/Uintan</b>
31	41.3	40.4	Bartonian/Uintan
32	40.4	38	Bartonian/Duchesnean
33	38	37.2	Bartonian/Chadronian
34	37.2	33.9	Priabonian/Chadronian

**Table 2** - List of faunas of the Indian subcontinent. Betweenness scores are for the bin

**Comment [TH16]:** R1a

indicated at a threshold of 0.5, and are the highest proportion of shortest routes obtained for that formation. Faunas with n/a values are those represented by too few taxa for Forbes faunal similarity calculations, or with no connections to other faunas at a threshold of 0.5, and therefore are not represented in the faunal networks.

	<b>Lithologic Unit</b>	<b>Age</b>	<b>Environment</b>	<b>Betweenness (Bin)</b>
Barmer Basin	Kapurdi	Early Eocene	Nearshore to shallow marine	72/3,655 (25)
	Akli	Late Paleocene to Early Eocene	Nearshore terrestrial	0/1,378 (22)
	Fatehgarh	Early Paleocene (Danian)	Nearshore to shallow marine	n/a
Jaisalmer Basin	Khuiala	Early Eocene (Ypresian)	Shallow marine	n/a
Western India	Harudi	Eocene	Lagoonal	0/1,485 (30)
	Naredi	Eocene	Terrestrial to shallow marine	42 (30)
	Intertrappean Beds	Late Cretaceous	Fluvio-lacustrine	17/6,670 (12)
	Lameta	Late Cretaceous	Fluvio-lacustrine	108/6,670 (12)
Cauvery Basin	Kallamedu	Late Maastrichtian	Fluvio-deltaic terrestrial	144/2,301 (13)
Cambay Basin	Cambay Shale	Early Eocene	Lagoonal to shallow marine	28/3,655 (25)
Himalayan Foreland Basin	Subathu	Eocene	Shallow marine to marine	42/4,950 (29)
Kala Chitta Hills	Kuldana	Eocene	Fluvio-deltaic to lagoonal	1,997/5,050 (33)
	Mami Khel	Eocene	Fluvio-deltaic	2/3,403 (26)
	Chorgali	Eocene	Shallow marine	0/1,485 (30)
Lower Indus	Ghazij	Early Eocene	Deltaic to shallow marine	41.5/4,095 (28)

Basin	Khadro	Paleocene	Coastal, shallow marine	n/a
	Pab	Late Cretaceous	Fluvial	25/6,670 (12)

## FIGURE LEGENDS

Figure 1. Global paleogeographic map during Late Cretaceous showing the main fossil localities mentioned in the text. 1, Lameta Formation (India); 2, Intertrappean (India); 3, Kallamedu Formation (India); 4, Pab Formation (Pakistan); 5, Maevarano Formation (Madagascar); 6, Ortega (Colombia); 7, Rognacian Formation (France).

Figure 2. Global paleogeographic map during Palaeocene showing the main fossil localities mentioned in the text. 1, Fatehgarh Formation (India); 2, Niniyur Formation (India); 3, Khadro Formation (Pakistan); 4, Akli Formation (India); 5, Aruma Formation (Saudi Arabia); 6, Umm Himar Formation (Saudi Arabia); 7, Hornerstown Formation (United States); 8, Santa Lucía Formation (Bolivia); 9, Cerrejón Formation (Colombia); 10, Jbel Guersif Formation (Morocco); 11, Itaboraí Formation (Brazil); 12, Soissonais Formation (France).

Figure 3. Global paleogeographic map during Eocene showing the main fossil localities mentioned in the text. 1, Cambay shale (India); 2, Naredi Formation (India); 3, Kapurdi Formation (India); 4, Khuiala Formation (India); 5, Mami Khel clay (Pakistan); 6, Ghazij Formation (Pakistan); 7, Sezanne-Broyes Formation (France); 8, Niushan Formation (China); 9, Suffolk pebble beds; 10, Willwood Formation (United States); 11, Gres d'Assignan (France); 12, Monte Bolca (Italy); 13, Tallahatta Formation (United States); 14, Subathu Formation (India); 15, Kuldana Formation (Pakistan); 16, Harudi Formation (India); 17, Chorgali Formation (Pakistan); 18, Irtysh River (China/Kazakhstan); 19, Grabels (France);

20, Yegua Formation (United States); 21, Shark River Formation (United States); 22, Elmore Formation (England); 23, Mokattam (Egypt).

Figure 4 – A graph with connections between all nodes (left) is a ‘complete’ graph, and has a density of one. The density of a graph is calculated as the proportion of the possible connections present. For example, the more structured graph on the right has seven of 15 present, and therefore has a density of 0.47.



Figure 5 – Faunal network of all Cretaceous to Eocene vertebrate sites, thresholded to 0.75 and with all unconnected localities removed. The strongest division is between Cretaceous (circle) and Paleogene (square) sites, followed by geographic divisions based on continents, represented by colours as follows: North America – green, Asia – sky blue, South America – navy blue, Europe – pink, the Indian subcontinent – red, Madagascar – dark orange, Africa – pale orange, Australia – yellow. 24 clusters can be identified, as follows: (i) Cretaceous Gondwana, (ii) the Shendi and Wadi Milk formations, (iii) Aquitaine Basin, (iv) Turonian-Campanian Utah, (v) Cretaceous Europe, (vi) Maastrichtian Patagonia and Antarctica, (vii) Campanian-Maastrichtian North America and East and Central Asia, (viii) Cretaceous global

shallow marine sites generally dominated by marine reptiles and sharks, (ix) Paleocene North America and Europe, (x), Early Eocene North America, Asia, and Europe, (xi) Fish-dominated marine faunas of the Eocene, (xii) Late Eocene Europe, (xiii) Eocene Peru, (xiv) Paleocene Mongolia, (xv) Paleogene North Africa, (xvi) Eocene northern Indian subcontinent, (xvii) Eocene Australia, (xviii) Paleocene China, (xix) Late Eocene North America and Asia, (xx) Paleogene Argentina and Brazil, (xxi) Marine mammal sites in the Indian subcontinent and Africa, (xxii) Wanghudun, (xxiii) Cretaceous-Paleogene boundary sites in the Indian subcontinent and South America, (xxiv) Eocene Asia. This cluster pattern is very well supported, with a modularity score of 0.76.

Figure 6 – Faunal network of Maastrichtian (Bin 13) vertebrate localities, threshold = 0.75. The network is divided into six clusters by edge betweenness. i – Ahlen and Dukamaje formations of Europe and Africa. ii – Most of Europe and Gondwana, including all localities on the Indian subcontinent. iii – Eastern Laurentia, including Mount Laurel, Marshalltown, Tar Heel formations, concentrating on marine taxa, hence also the Palmyra Phosphates. iv – High latitude localities from Canada, Russia, and New Zealand. v – Terrestrial North America, mostly around the Western Interior Seaway, as well as East Asian localities. vi – Mongolia and China, along with a single South American site – Lago Colhue Huapi. Colours are as in Figure 5.

Figure 7 – Faunal network of the Early Eocene (Bin 25), threshold = 0.75. The network is divided into eight identifiable clusters. i – South America, ii – Grès d'Assignan and La Borie, France, iii – Other French Eocene sites, iv – Cambay Shale, connected to Asia and France, v – Large group comprising North America and mostly non-French European sites, vi – Wutu

and the Calcaires des Montaigues, vii – East Asia, viii – Marine (Bashi, Nanjemoy, Kapurdi). Colours are as in Figure 5.

Figure 8 – Faunal network of the Late Eocene (Bin 33), threshold = 0.75. The network is divided up into seven identifiable clusters. i – Asia (and the Pruett Formation of the USA), ii – North America (and the Ube Formation of Japan), iii – The Kuldana and Iwaki formations and the Shangqinglong fissure fill site, iv – Marine (Jackson and Yazoo formations, USA), v – Argentina, vi – Peru, vii – Europe (and the Wind River Formation of the USA). Colours are as in Figure 5.