

Research



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Global biogeography since Pangaea

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The break-up of the supercontinent Pangaea around 180 Ma has left its imprint on the global distribution of species and resulted in vicariance-driven speciation. Here, we test the idea that the molecular clock dates, for the divergences of species whose geographical ranges were divided, should agree with the palaeomagnetic dates for the continental separations. Our analysis of recently available phylogenetic divergence dates of 42 pairs of vertebrate taxa, selected for their reduced ability to disperse, demonstrates that the divergence dates in phylogenetic trees of continent-bound terrestrial and freshwater vertebrates are consistent with the palaeomagnetic dates of continental separation.

1. Introduction

Biogeographers from Darwin to Darlington have been primarily concerned with illuminating the routes and mechanisms responsible for the present-day distributions of organisms [1]. Disjunct distributions can be explained either by fragmentation of ancestral biogeographic ranges by vicariant (isolating) events or by dispersal across a pre-existing barrier (e.g. an ocean) [2]. There is an on-going debate about the relative importance of these two hypotheses.

When a landmass breaks up due to continental drift, the geographical ranges of thousands of species are simultaneously divided [1]. Vicariance-driven speciation is followed by radiation on each side of the break-up. Subsequently, over millions of years, pairs of geographically separated taxa emerge from the original species. Each pair of these sister taxa will have a divergence time from a common ancestor that should correspond to the time of the continental break-up. The recent explosion in the number of species with sequenced genomes includes many species that belong to the geographically separated sister taxa. These sequences permit construction of well-calibrated phylogenetic trees and molecular-clock-based estimates of the divergence times of those taxa [3,4]. Our goal is to verify that divergence dates based on molecular clocks correlate with palaeomagnetic dates for the continental separations, and to help quantify the extent of their agreement.

Previous palaeobiogeographic research has been either taxon-specific (e.g. Platnick's spiders [5]; Mittermeier's birds [6]; Zhang *et al.*'s frogs [7]) or continent-specific (e.g. Tabuce *et al.*'s Afrotheria [8]; Gibb *et al.*'s Xenarthra [9]; Hu *et al.*'s Laurasiatheria [10]). Here, we analyse the global chronology of biogeographic divergences from published phylogenies [3,4] of 42 vertebrate taxa pairs and compare them with palaeomagnetic dates for the break up of Pangaea.

Pangaea began to separate around 180 Ma (figure 1) into a southern continent, Gondwana (which contained what is now South America, Africa, India, Madagascar, Australia, New Zealand and Antarctica), and a northern continent, Laurasia (which contained what is now North America, Europe and Asia, minus the Indian subcontinent). Subsequently, Gondwana and Laurasia each split to produce the present biogeography. Thus, the morphological similarities of pairs of relatively immobile taxa from South America and Africa are not the result of the dispersal of several hundred species across the Atlantic by rafting, but instead result from both faunas being descendants of the same ancestral biota that split around 100 Ma.

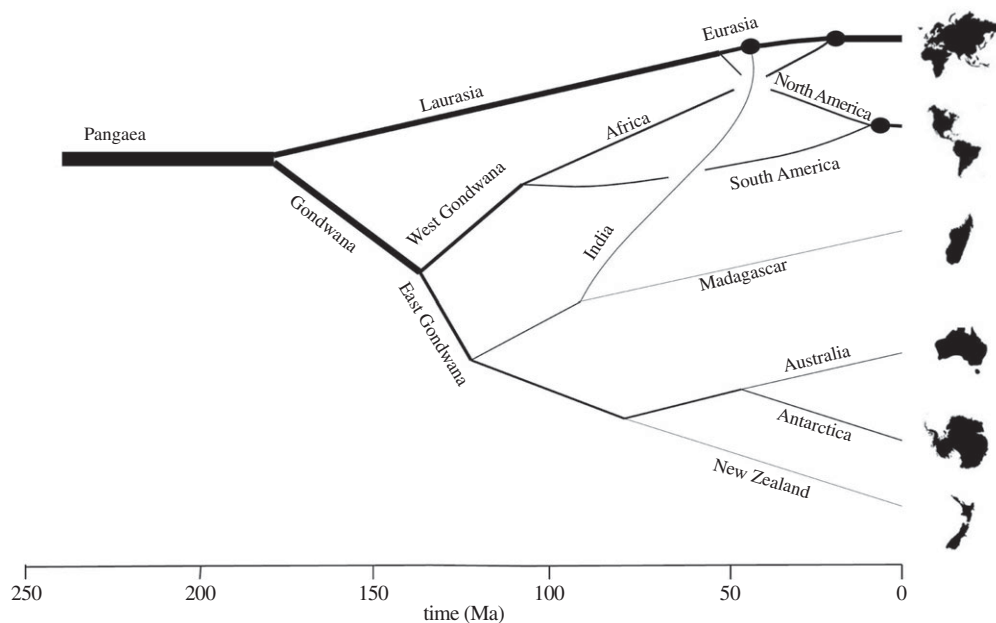


Figure 1. Simplified sketch of the break-up of the supercontinent Pangaea over the past 180 Myr. Geological and biological chronologies provide two independent ways to date eight continental divergences and three continental convergences. Continental separations are more complicated than shown here [11]. They are not instantaneous and occur over tens of millions of years (electronic supplementary material, table S1, column 7). Such durations are comparable with the amount of correlation between the palaeomagnetic and phylogenetic divergence dates, and set a lower limit to the expected level of agreement. Circles indicate continental collisions. Line thickness is a rough proxy for landmass area.

2. Results and analysis

The plate tectonic history of Pangaea has been well documented using palaeomagnetic dating. The chronology of the break-up of Pangaea presented here (figure 2a) is based on the weighted average of four palaeomagnetic data sources for each of eight continental separations and three continental collisions (electronic supplementary material, table S1).

Thousands of species have had their geographical ranges divided by continental movements. Most of these species went extinct either on one or both sides of the division; extant endemic sister taxa, on separated continents, were required to analyse the vicariance phenomenon. Some species could have diverged before continental break-up, but with small-number statistics these are difficult to identify. Fossil-based attempts at a global biogeographic analysis have been compromised due to the sparseness of the fossil record and the fact that fossils (unlike molecular clocks) usually provide only minimum age constraints on continental divergence times [12]. The timetree.org database [3,4], which has assembled a comprehensive sample of phylogenetic molecular clock divergence dates from the current literature, despite being heterogeneous in quality, sampling and calibration, presents the best current compendium and has been used in our analysis (electronic supplementary material, table S2). While the most common evidence for the three continental collision events (India + Eurasia, Africa + Eurasia and North + South America) was fossil data, endemic species dispersal to the new continent and their subsequent diversification (traced phylogenetically) was also used to indicate a migration event.

To minimize the amount of over-water dispersal of the taxon across continents, divergence and collision data groups were selected according to the following criteria:

- The group must consist only of continent bound terrestrial and freshwater vertebrates.
- The group must be monophyletic.
- The group must be represented in at least two of the continents.

We have reviewed the current literature and selected a substantial (but not exhaustive) list of groups fitting these criteria. Molecular divergence dates from 42 pairs of vertebrate sister taxa (labelled 1–42), derived from over 500 species, are shown in figure 2b. Continental collision dates were biologically evaluated using the biotic interchange data from 14 vertebrate taxa (labelled 43–56 in figure 2b), derived from over 100 species.

Our analysis primarily focused on ancient vicariant events related to plate tectonic movements, so it was important that phylogenetic divergences were not due to dispersal (e.g. by rafting or island hopping). For example, there is a controversy over the origin of the mammalian fauna of Madagascar [13–15]. Several Late Oligocene to Mid-Eocene (approx. 26–50 Ma) terrestrial mammalian groups in Madagascar are closely related to those found in Africa [16]. Molecular clock data indicate that the tenrecs would have begun diversification at 20–32 Ma, the nesomyines (Malagasy rodents) at 18–30 Ma, and the Malagasy carnivores at 14–25 Ma [17]. One proposal regarding the origin of these mammals on Madagascar suggests the brief existence of a land bridge, along the Davie Ridge fault line, during this period (but there is evidence against this proposal [18]); others have assumed dispersal across the Mozambique channel [17,19].

These Madagascar mammals fit the vicariance selection criteria; however, they are clearly the result of dispersal. To account for this phenomenon, we need to further limit our parameters.

The less mobile the species, the more likely its divergence into two species resulted from continental separation. To minimize the effect of large-scale dispersal across oceans, taxa were selected for their reduced ability to have undergone dispersal-driven speciation. Therefore, we specifically selected continent-bound terrestrial and freshwater vertebrates (figure 2b). To further limit the effects of dispersal on our dataset, we have created an immobility index to help quantify the extent to which each of the vertebrate taxa were continent bound. The mobility of the taxa depends on many intrinsic

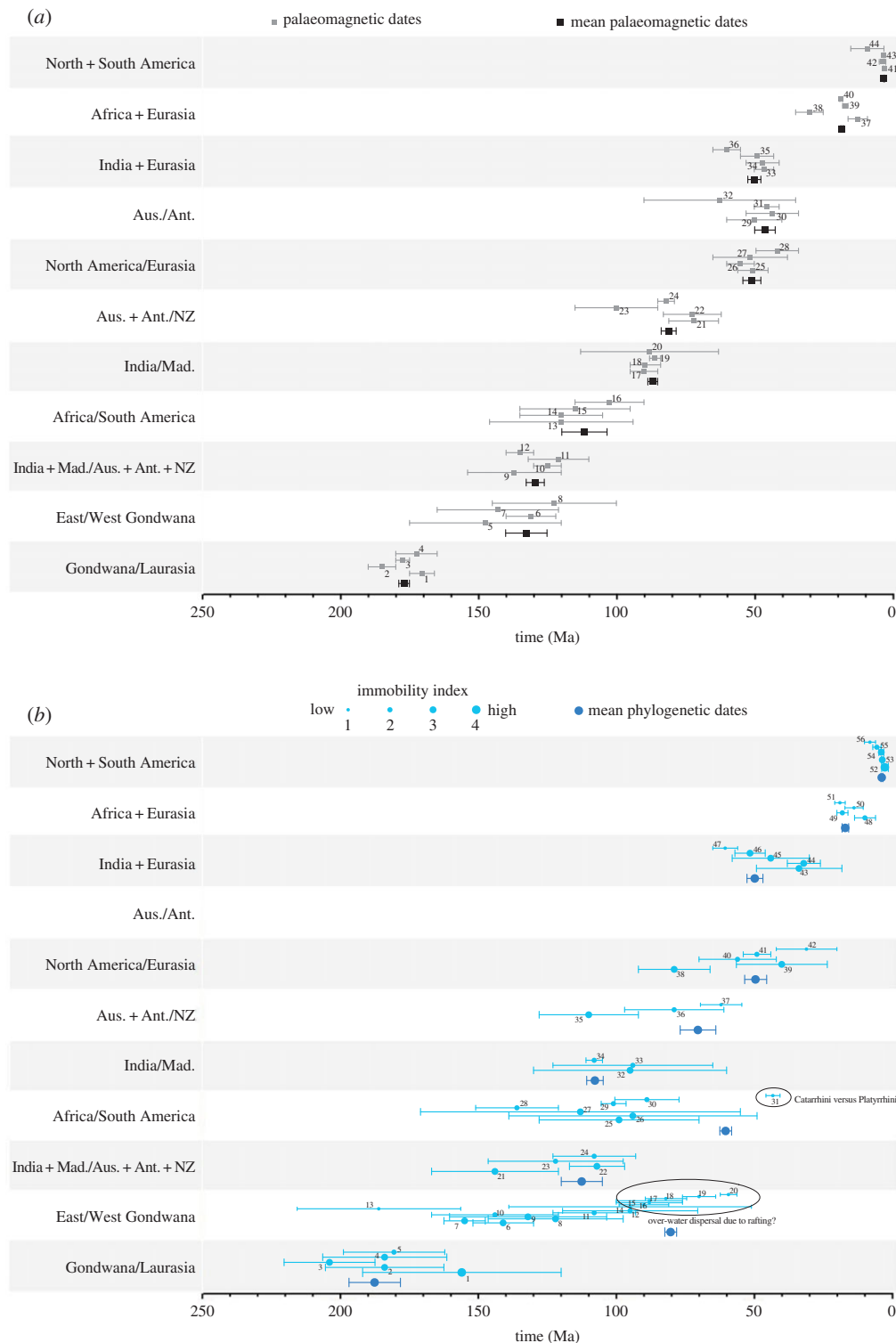


Figure 2. (a) Palaeomagnetic dates for continental divergences and collisions. Numerical labels (1–44) refer to references (electronic supplementary material, table S1). In (b), we plot molecular clock divergence dates of speciation associated with continental divergences (1–42) and biotic interchange dates associated with continental collisions (43–56) (electronic supplementary material, table S2). No phylogenetic data from the Australia/Antarctica divergence is applicable; thus, this divergence is represented by only palaeomagnetic data. Point sizes of phylogenetic data indicate the immobility index for that pair of taxa (table 1; electronic supplementary material, table S2).

(e.g. body condition) and extrinsic (e.g. climate) factors [20]. The four immobility factors described in table 1 were assessed for each of the 42 divergence pairs and 14 collision vertebrate taxa (electronic supplementary material, table S2).

Continent-bound, immobile species were assigned a high immobility index of $I = 4$. More mobile species (that might be able to disperse across an ocean) were assigned an immobility index of $I = 1$. We estimated the immobility index for each pair of taxa (electronic supplementary material, table S2)

without reference to its divergence date. Then, in figure 2b, we plotted divergence dates and used point size to indicate the immobility index.

Inclusion of mobile species able to navigate across broad ocean channels and survive in diverse environments would systematically shift the biology-based divergence to more recent times.

This tendency can be seen in the points labelled 15 through 20 (figure 2b), in the East/West Gondwana divergence (inside

Table 1. Immobility factors.

immobility factors	reasoning	example
dispersal restraints	The species would need to endure a sea voyage including exposure to saltwater and fluctuating temperatures. If the species is salt or temperature sensitive, it might not survive long enough to disperse across and populate the new continent.	freshwater fish and selective frogs
dietary requirements	For a species to survive crossing a continental divide it would need to be flexible enough with its diet to find satisfactory food sources on the sea voyage and upon arrival in the new ecosystem. Species in a commensal or symbiotic relationship would have difficulty adapting without their partners.	specific fish, geckos and caecilians
reproduction limitations	Some animals reproduce rapidly and produce many offspring (<i>r</i> -selection). With only one pregnant female, these animals could rapidly colonise a new continent. Others do not reach sexual maturity for many years after birth and then produce few offspring (<i>K</i> -selection), and would be less likely to colonise a new continent.	primates and mammals
mating limitations	Seasonal breeders successfully mate only during certain times of the year. These mating periods result in births at times optimal for survival of the young, taking into account factors such as ambient temperature, food and water availability, and changes in predation behaviours of other species.	selective mammals, fish and frogs

the oval labelled ‘over-water dispersal due to rafting?’) for which $I = 1$. Another outlier is the Catarrhini/Platyrrhini taxa pair (31) associated with the Africa/South America divergence. These are highly mobile primates that were assigned a low immobility index of $I = 1$. Separation of these two taxa could be ascribed to over-water dispersal millions of years after continental split. On the opposite side of the immobility spectrum the African torrent frog versus neotropical true frog (30) was assigned a high immobility index because, in general, frogs are intolerant of salt water. The taxa pair *Gymnopsis* (American caecilians) versus *Ichthyophis* (Asian caecilians) in the Gondwana/Laurasia divergence is an example of the highest immobility, which is due to their intolerance of salt water, in which, like most amphibians, they suffer desiccation. High immobility may also be due to their burrowing lifestyle (see however [21]). For continental collisions, as continents moved closer together, more mobile species could have dispersed before the collision occurred. Thus, $I = 1$ points in collisions should have older dates. A slight tendency in this direction is seen for the $I = 1$ points for the three collisions at the top of figure 2b.

We have combined the data in figure 2 to produce figure 3 with the following modifications. To isolate the effect of vicariance, we needed to reduce the possibility of dispersal. All $I = 1$ points were excluded, and the immobility index was used to modify variance of the remaining biology points such that when computing the weighted average, mobile taxa were down-weighted and immobile taxa had more weight (equation (4.1)).

From figure 3, there does not appear to be a kink at the K-Pg extinction event (around 66 Ma), indicating that our examples of continental drift-driven vicariant speciation do not seem to be affected by mass extinction boundaries; as opposed to the rapid radiation effect these events have on dispersal-driven speciation [22].

In figure 4, time averages from palaeomagnetism (x -axis, black horizontal error bars) and phylogeny (y -axis, blue vertical error bars) are highly correlated (0.98 correlation coefficient). For most points, uncertainties for the palaeomagnetic

values are smaller than analogous phylogenetic uncertainties. Notable exceptions include the approximately equal length of both vertical and horizontal error bars for East/West Gondwana and Africa/South America. These highly correlated results also demonstrate that whole-sequence molecular clocks give the expected results for known times of continental break up and continental collisions, and provide independent support for the approximate validity of molecular clocks.

3. Discussion and conclusion

There is much evidence that dispersal (rather than vicariance) has played an important role in establishing disjunct biogeographic distributions (e.g. *Perca* crossing the Bering land bridge [21], or the dispersal of the *Amphisbaenia* throughout the Americas, Europe and Africa, despite their high immobility [21]). In addition, there is evidence for several transcontinental distributions due to dispersal after the K-Pg extinction, such as booid snakes, ungulates and primates, and cryptobranchid and amphiumid salamanders [23–27]. While dispersal may be a common method of speciation, we have used our immobility index to minimize its role. Our result in figure 4 shows that vicariance due to continental drift has played a significant role.

There are several nuances regarding the splitting of the continents (e.g. land bridges) that could alter the continental movements presented in this paper. For example, there is an ongoing polemic over whether New Zealand was above sea-level for the entirety of its isolation, or was submerged, and only populated by dispersal upon re-emergence [28]. Glaciation and stream capture provide ephemeral modifications to the ability to disperse, but not on the time and space scale relevant here. Future systematic improvements will result in reduced uncertainty for the palaeomagnetic dates [29]. Furthermore, increases in the number of species with full genomes and improvements to molecular clock calibrations should reduce uncertainties on the phylogeny-based divergence times.

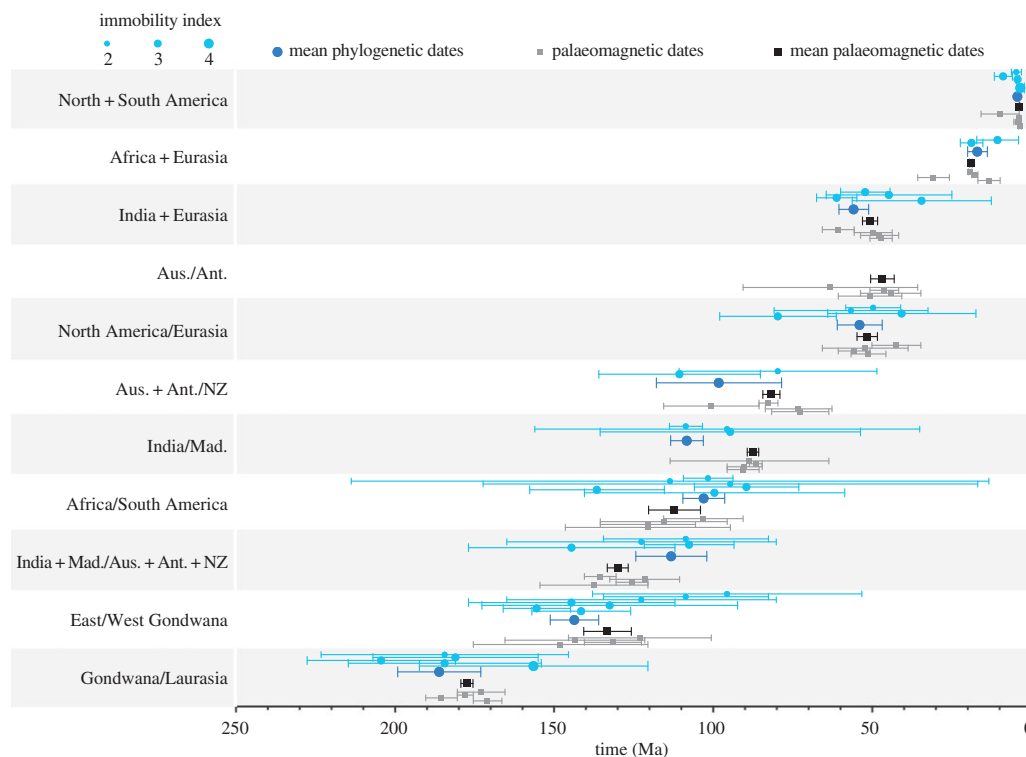


Figure 3. Phylogenetic and palaeomagnetic data modified from figure 2. The most mobile taxa with immobility index $I = 1$ are excluded. We used the immobility index (through equation (4.1)) to modify variances for computing phylogenetic mean values.

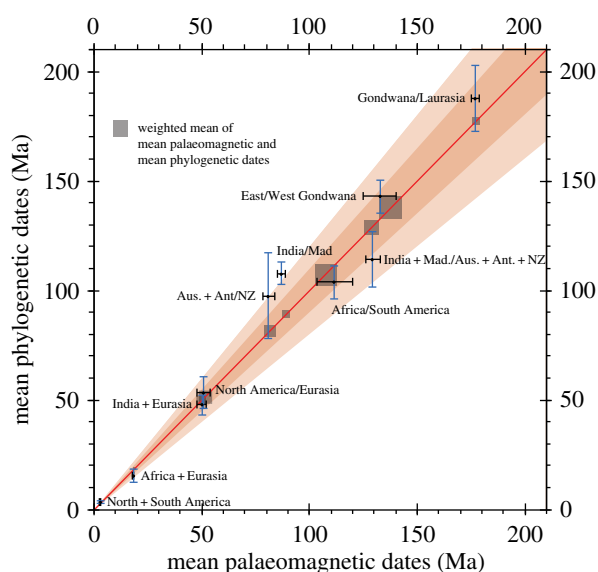


Figure 4. Comparison of the mean palaeomagnetic dates with the mean phylogenetic dates. Weighted means of the two independent estimates are represented by grey squares along the diagonal (electronic supplementary material, table S3). With perfect agreement, all points would lie on the red line with slope = 1. Slopes of the dark and light orange wedges are 1 ± 0.1 and 1 ± 0.2 , respectively. Error bars in the vertical and horizontal directions for East/West Gondwana and Africa/South America have approximately equal length. Thus, phylogenetic data are becoming of equal importance in dating continental divergences.

With continually improving techniques for estimating both palaeomagnetic continental break-up dates and molecular-clock-based phylogenetic dates, a more precise and accurate comparison can be made, not only for Pangaea but potentially for the break-up of earlier supercontinents, such as Pannotia (*ca* 545–600 Ma) and Rodinia (*ca* 1.1–0.75 Ga).

4. Material and methods

(a) Immobility index

Our immobility index assigns values between 1 and 4—with 1 assigned to the most mobile taxa and 4 to the least mobile. When computing weighted averages in figure 3, we exclude pairs of taxa with immobility 1, and assign more weight to pairs with the highest immobility, as they have divergence dates that are less likely to result from dispersal. Specifically, we increased the reported variance of a phylogenetic divergence date σ_{bi}^2 depending on the immobility index as follows:

immobility index	modification of variance	} (4.1)
4	$\sigma_{bi}^2 \rightarrow 1 \sigma_{bi}^2$	
3	$\sigma_{bi}^2 \rightarrow 2 \sigma_{bi}^2$	
2	$\sigma_{bi}^2 \rightarrow 3 \sigma_{bi}^2$	
1	excluded.	

With these modifications to σ_{bi}^2 , we computed inverse variance-weighted means in the same way as for the geological data. Let g_i and b_i be the geology and biology inverse-variance-weighted average dates for the i th continental break-up (or collision). Let σ_{gi}^2 and σ_{bi}^2 be their variances, respectively (after the σ_{bi}^2 have been modified as described in equation (4.1)). Let t_i be the weighted average of b_i and g_i :

$$t_i = \frac{b_i/\sigma_{bi}^2 + g_i/\sigma_{gi}^2}{1/\sigma_{bi}^2 + 1/\sigma_{gi}^2}. \quad (4.2)$$

(b) χ^2 -test

We used χ^2 per degree of freedom ($\chi^2/\text{d.f.}$) tests to provide some justification for our reported uncertainties. For example, the palaeomagnetic literature reports ranges that we take as ‘1 sigma’ ranges or 68% confidence intervals. For each of the 11 nodes in the electronic supplementary material, table S1, we compute $\chi^2/\text{d.f.}$ The average of these 11 values is approximately 1. Similarly, $\chi^2/\text{d.f.}$ values for the 10 nodes in the electronic

supplementary material, table S2 (after removal of the $I = 1$ data) suggest that uncertainties reported on the TTOL (Time Tree Of Life) values in timetree.org can be plausibly taken as 68% confidence intervals. To determine whether b_i and g_i are consistent with t_i , we compute χ^2 (equation (4.3)) and verify that $\chi^2/\text{d.f.} \sim 1$.

$$\chi_{\text{total}}^2 = \sum_{i=1}^N \frac{(b_i - t_i)^2}{\sigma_{b_i}^2} + \sum_{i=1}^N \frac{(g_i - t_i)^2}{\sigma_{g_i}^2}, \quad (4.3)$$

where $N = 10$. See the last two columns of electronic supplementary material, table S3.

References

1. Crisci J, Katinas L, Posadas P, Crisci JV. 2009 *Historical biogeography: an introduction*. Cambridge, MA: Harvard University Press.
2. Sanmartín I. 2003 Dispersal vs. vicariance in the Mediterranean: historical biogeography of the Palearctic Pachydeminae (Coleoptera, Scarabaeoidea). *J. Biogeogr.* **30**, 1883–1897. (doi:10.1046/j.0305-0270.2003.00982.x)
3. Kumar S, Hedges SB. 2016 TimeTree database. Temple University. Accessed 5 December 2016. See <http://www.timetree.org/>.
4. Hedges SB, Marin J, Suleski M, Paymer M, Kumar S. 2015 Tree of life reveals clock-like speciation and diversification. *Mol. Biol. Evol.* **32**, 835–845. (doi:10.1093/molbev/msv037)
5. Platnick NI. 1976 Drifting spiders or continents?: Vicariance biogeography of the spider subfamily Laroniinae (Araneae: Gnaphosidae). *Syst. Biol.* **25**, 101–109. (doi:10.2307/2412735)
6. Mittermeier JC. 2014 Avian biogeography and conservation in Eastern Indonesia. Doctoral dissertation, University of Oxford, UK.
7. Zhang P, Liang D, Mao RL, Hillis DM, Wake DB, Cannatella DC. 2013 Efficient sequencing of anuran mtDNAs and a mitogenomic exploration of the phylogeny and evolution of frogs. *Mol. Biol. Evol.* **30**, 1899–1915. (doi:10.1093/molbev/mst091)
8. Tabuce R *et al.* 2007 Early Tertiary mammals from North Africa reinforce the molecular Afrotheria clade. *Proc. R. Soc. B* **274**, 1159–1166. (doi:10.1098/rspb.2006.0229)
9. Gibb GC, Condamine FL, Kuch M, Enk J, Moraes-Barros N, Superina M, Poinar HN, Delsuc F. 2016 Shotgun mitogenomics provides a reference phylogenetic framework and timescale for living xenarthrans. *Mol. Biol. Evol.* **33**, 621–642. (doi:10.1093/molbev/msv250)
10. Hu J, Zhang Y, Li Y. 2013 Summary of Laurasiatheria (mammalia) phylogeny. *Zool. Res.* **33**, E65–E74. (doi:10.3724/SP.J.1141.2012.E05-06E65)
11. EarthByte. 2017 GPlates 1.5 software and datasets. See http://www.earthbyte.org/Resources/earthbyte_gplates.html.
12. Parham JF *et al.* 2012 Best practices for justifying fossil calibrations. *Syst. Biol.* **61**, 346–359. (doi:10.1093/sysbio/syr107)
13. Reddy S, Driskell A, Rabosky DL, Hackett SJ, Schulenberg TS. 2012 Diversification and the adaptive radiation of the vangas of Madagascar. *Proc. R. Soc. B* **280**, 20112380. (doi:10.1098/rspb.2011.2380)
14. Gunnell GF. 2013 Biogeography and the legacy of Alfred Russel Wallace. *Geol. Belg.* **16**, 211–216.
15. Crottini A, Madsen O, Poux C, Strauß A, Vieites DR, Vences M. 2012 Vertebrate time-tree elucidates the biogeographic pattern of a major biotic change around the K–T boundary in Madagascar. *Proc. Natl Acad. Sci. USA* **109**, 5358–5363. (doi:10.1073/pnas.1112487109)
16. Rabinowitz PD, Woods S. 2006 The Africa–Madagascar connection and mammalian migrations. *J. Afr. Earth Sci.* **44**, 270–276. (doi:10.1016/j.jafrearsci.2005.12.005)
17. Chatterjee HJ, Ho SY, Barnes I, Groves C. 2009 Estimating the phylogeny and divergence times of primates using a supermatrix approach. *BMC Evol. Biol.* **9**, 1. (doi:10.1186/1471-2148-9-259)
18. Klimke J, Franke D. 2016 Gondwana breakup: no evidence for a Davie Fracture Zone offshore northern Mozambique, Tanzania and Kenya. *Terra Nova* **28**, 233–244. (doi:10.1111/ter.12214)
19. Masters JC, De Wit MJ, Asher RJ. 2006 Reconciling the origins of Africa, India and Madagascar with vertebrate dispersal scenarios. *Folia Primatol.* **77**, 399–418. (doi:10.1159/000095388)
20. Bowler DE, Benton TG. 2005 Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol. Rev.* **80**, 205–225. (doi:10.1017/S1464793104006645)
21. Carney JP, Dick TA. 2000 The historical ecology of yellow perch (*Perca flavescens* [Mitchill]) and their parasites. *J. Biogeogr.* **27**, 1337–1347. (doi:10.1046/j.1365-2699.2000.00511.x)
22. Harries PJ, Kauffman EG, Hansen TA. 1996 Models for biotic survival following mass extinction. *Geol. Soc. Spec. Publ.* **102**, 41–60. (doi:10.1144/GSL.SP.1996.001.01.03)
23. Longrich NR, Vinther J, Pyron RA, Pisani D, Gauthier JA. 2015 Biogeography of worm lizards (*Amphisbaenia*) driven by end-Cretaceous mass extinction. *Proc. R. Soc. B* **282**, 20143034. (doi:10.1098/rspb.2014.3034)
24. Longrich NR, Bhullar BAS, Gauthier JA. 2012 Mass extinction of lizards and snakes at the Cretaceous–Paleogene boundary. *Proc. Natl Acad. Sci. USA* **109**, 21396–21401. (doi:10.1073/pnas.1211526110)
25. Clemens WA. 2002 Evolution of the mammalian fauna across the Cretaceous–Tertiary boundary in northeastern Montana and other areas of the Western Interior. *Geol. Soc. Spec. Publ.* **361**, 217–245. (doi:10.1130/0-8137-2361-2.217)
26. Naylor BG. 1981 Cryptobranchid salamanders from the Paleocene and Miocene of Saskatchewan. *Copeia* **1981**, 76–86. (doi:10.2307/1444042)
27. Gardner JD. 2003 The fossil salamander *Proamphiuma cretacea* Estes (Caudata; Amphiumidae) and relationships within the Amphiumidae. *J. Vert. Paleo.* **23**, 769–782. (doi:10.1671/1828-4)
28. Claramunt S, Cracraft J. 2015 A new time tree reveals Earth history's imprint on the evolution of modern birds. *Sci. Adv.* **1**, e1501005. (doi:10.1126/sciadv.1501005)
29. Heslop D, Roberts AP. 2016 Estimation and propagation of uncertainties associated with paleomagnetic directions. *J. Geophys. Res. Solid Earth* **121**, 2274–2289. (doi:10.1002/2015JB012544).

Data accessibility. All data are supplied as the electronic supplementary material.

Authors' contributions. S.R.N.M. and C.H.L. did the analysis. C.P.G. and S.R.N.M. were responsible for the immobility index. All authors contributed to the writing of the manuscript.

Competing interests. We declare we have no competing interests.

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