Palaeogeography, Palaeoclimatology, Palaeoecology xxx (2015) xxx–xxx

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Madagascar's climate at the K/P boundary and its impact on the island's biotic suite

Masamichi Ohba [a,1], Karen E. Samonds [b], Marni LaFleur [c], Jason R. Ali [d], Laurie R. Godfrey [e,*]

[a] Central Research Institute of Electric Power Industry (CRIEPI), Environmental Science Research Laboratory, 1646 Abiko, Abiko-shi, Chiba 270-1194, Japan
[b] Department of Biological Sciences, Northern Illinois University, DeKalb, IL 60115, USA
[c] University of Veterinary Medicine Vienna, Veterinarplatz 1, 1210 Vienna, Austria
[d] Department of Earth Sciences, University of Hong Kong, Pokfulam Road, Hong Kong, China
[e] Department of Anthropology, University of Massachusetts, 240 Hicks Way, Amherst, MA 01003, USA

ARTICLE INFO

Article history:
Received 16 June 2015
Received in revised form 1 October 2015
Accepted 18 October 2015
Available online xxxx

Keywords:
Madagascar
Biogeography
Origin
Evolution
K/P boundary
Dispersal
Paleogene

ABSTRACT

The K/P boundary, 66 Ma, was a critical time in the history of the planet's biota. On the island of Madagascar, few Late Cretaceous species survived the associated extinction, and distance from the various mainland sources then acted as a strong filter for the number of over-water arrivees. Reconstructing the climate of the early Paleogene is vital for understanding the environments to which new colonizers landed and established a toe-hold on the island. Beginning with a "global" air-sea-coupled climate model simulation using the land–sea distribution at 66 Ma, we used dynamical downscaling to construct a scenario for how the atmospheric and oceanic fluid envelopes washed over and around the Madagascar at the start of the Paleocene. Dynamical downscaling of the global model yields a climate model with much finer resolution. We used this method to reconstruct the habitats for known fossil localities from that general period, better understand the ecological diversity of plants and animals that have been hypothesized to have then been present, and evaluate hypotheses regarding the evolutionary history of lemurs—a vast clade of primates endemic to Madagascar whose last common ancestor dates to this time. Our results show an island with a climate notably different from that of today, but not nearly as arid as others have suggested: the spiny thicket biome did not exist; temperatures were lower; rainfall less seasonal.

1. Introduction

During the great global extinction at the K/P boundary, 66 Ma, Madagascar, like other land masses on the planet, suffered major faunal loss. Most of the unusual, endemic animals for which this island is famous today, including its iconic lemurs, are the descendants of colonizers that began arriving shortly afterwards. What sort of world did these colonizers inhabit? Was the island very arid? How did the climate at this critical time in the evolutionary history of Madagascar's fascinating biota help shape the recovery following the devastating extinctions of dinosaurs and other animals, and mold the future of survivors and new colonizers?

While it is generally understood that Madagascar in the early Paleogene was "arid," relatively little is actually known about the climate of the island at the time and how it affected the fauna and flora. Furthermore, many of the taxa that survived the K/P extinction or arrived shortly afterwards cannot be characterized as dry-loving. The notion that, from the Late Cretaceous through the end of the Eocene, Madagascar was moisture restricted is derived largely from the analysis of Wells (2003), who noted that the island would have been located >1600 km south in the zone of high-atmospheric-pressure deserts and concluded that only drought-adapted organisms could then have flourished. As also argued by Koechlin (1972), Wells (2003) suggested that the flora would have been dominated by spiny bush or thicket, which is today restricted to the southwest of the island. He further argued that the spiny thicket coverage would have contracted in the Eo–Oligocene as Madagascar drifted northwards into the wetter trade wind belt. Furthermore, he maintained that 1) wet and dry deciduous forests would have begun replacing arid bush habitats only after the mid-Paleocene, 2) the eastern rain forests did not exist until well into the Eocene or Oligocene, and 3) the northwestern monsoon forests did not exist until the late Miocene or Pliocene, first in the highlands and then spreading into the lowlands. Critically, however, Wells (2003)) failed to explain the mismatch between the assumed dry climate of the Late Cretaceous/early Paleogene and the moisture-loving nature of some of the island's known or inferred contemporary fauna and flora.

To address this issue, we simulated the climate at the K/P boundary time on Madagascar through a regional climate model. Using this reconstruction, we evaluate inferences regarding the depositional environments of known Upper Cretaceous and lower Paleogene fossil localities, and the ecological diversity of plants and animals that have

---

[*] Corresponding author.
E-mail addresses: oba-m@criepi.denken.or.jp (M. Ohba), ksamonds@niu.edu (K.E. Samonds), marni.lafleur@gmail.com (M. LaFleur), jrali@hku.hk (J.R. Ali), lgodfrey@anthro.umass.edu (L.R. Godfrey).
[1] Tel.: +81 70 5577 4802; fax: +81 4 7183 2966.

http://dx.doi.org/10.1016/j.palaeo.2015.10.028

Please cite this article as: Ohba, M., et al., Madagascar's climate at the K/P boundary and its impact on the island's biotic suite, Palaeogeogr. Palaeoclimatol. Palaeoecol. (2015), http://dx.doi.org/10.1016/j.palaeo.2015.10.028

been hypothesized to have been present. For the early Paleogene colonizers, we consider the environmental contexts under which important synapomorphies may have arisen. Taxa dating back to this time in Madagascar may be represented today by descendant clades that radiated appreciably later, under very different climatic conditions. Understanding the sequential appearance of synapomorphic traits in their selective contexts depends not merely on good phylogenetic reconstructions but on our ability to reconstruct changes in climate and habitats over time.

Ohba and Ueda (2010) conducted a global climate simulation for the Cretaceous using a "global" air-sea-coupled climate model consisting of the atmospheric general circulation and a simple ocean surface model. To this, they incorporated the changed continental configuration, including information regarding the break-up of Gondwana and the dispersion of the various continental blocks. Applying this simulation, they constructed climate snap-shots for periods of interest, including the K/P boundary. Global climate models such as these, however, cannot simulate synoptic-scale weather very well. In order to build a more detailed reconstruction of the Late Cretaceous climate for the southwest Indian Ocean region, dynamical downscaling of the global model output is required, as this enables high-resolution localized (c. 10 × 10 km) climate information to be extracted from relatively coarse-resolution global-scale (150–300 km by 150–300 km) models.

2. Materials and methods

Dynamical downscaling is achieved by applying a regional climate model to a global climate model output (for our purposes, the simulation of Ohba and Ueda, 2010). The regional climate model used here is the Weather Research and Forecasting Model (WRF) version 3.2.1 developed at the National Center for Atmospheric Research (NCAR) in Boulder, Colorado, USA. This model simulates the evolution of "weather conditions (such as precipitation, pressure, temperature, and wind)" from boundary forcing data generated by a global climate model or from direct observations. We used Madagascar's modern topography (and land-use condition) to simulate Madagascar at the K/P boundary (Suppl. Fig. 1), as the island's topography has changed relatively little since 66 Ma (Maarten de Wit, personal communication), despite minor episodes of tectonic activity (de Wit, 2003; Wells, 2003; Kusky et al., 2010). The last major phase of tectonic activity was associated with the Indian subcontinent rifting away ~85 Ma, which notably generated the prominent eastern escarpment (Chand and Subrahmanyam, 2003). Critically, Madagascar's central highlands were tectonically stable throughout the Cenozoic (Emmel et al., 2006, 2012).

We performed three experiments. The first was a present climate control experiment. We simulated the weather conditions in Madagascar during 2008 using the initial and lateral boundary conditions derived from the 6-hourly Japanese 25-year ReAnalysis (JRA-25) dataset (Onogi et al., 2007). It is difficult to model Madagascar's climate on the basis of multiple years because of the lack of computational resources. We selected 2008 as our reference year because there were no significant Indian Ocean basin-wide or dipole mode events in that year. The resolution of our regional climate model was about 15 km and the model domain was about 30°–60°E, 36°–6°S that was centered on Madagascar. The grid points were interpolated at 0.07° intervals for visualization. The vertical grid has 35 layers. The physics parameterizations adopted included the Kain–Fritsch cumulus convection scheme, Morrison 2–moment cloud microphysics scheme, Dudhia shortwave radiation scheme, rapid radiative transfer model long-wave radiation scheme, Yonsei University planetary boundary layer scheme, and Noah land surface model. The regional model WRF was driven using an atmospheric forcing dataset interpolated from the 6-hourly JRA-25 data (wind, humidity, temperature, geopotential height, surface pressure, and sea surface temperature). The four outermost rows of the grid points from the lateral boundary were nudged to the forcing data set.

The second experiment employed the same regional climate model but for the end of the Cretaceous (66 Ma), following Ohba and Ueda (2010). This takes into consideration the changes in the mean atmospheric fields of Madagascar 66 Ma and today by evaluating the impact of continental drift. The basic paleogeographic model was developed by JRA following Ali and Aitchison (Ali and Aitchison, 2008) originally published in Ali and Krause (2011). An image was constructed using the GMAP software (Torsvik and Smethurst, 1999). The basic block outlines were positioned using the plate motion and rotation parameters presented in Schettino and Scotese (2005). The paleoshorelines were added using Smith et al. (1994). The domain of the model was shifted (15° southward and 5° westward) to reflect the position of Madagascar 66 Ma ago. In other words, we used the same land–sea configuration for experiments 1 and 2 but shifted it horizontally in experiment 2. In the initial and lateral boundary conditions of the 66 Ma simulation, the differences between 66 Ma and present climate for the 30-year monthly mean GCM (general circulation model) data were added to the 6-hourly JRA data for each month in the present climate. This method allowed us to reduce the bias in the global climate model, and to simulate weather details for Madagascar at 66 Ma. The 66 Ma simulation thus applies the mean atmospheric fields in the 66 Ma model to the boundary perturbations of the present climate. The effect of the CO_2 concentration change is included in the boundary forcing of WRF obtained from Ohba and Ueda's model; the CO_2 concentration for the K/P boundary is assumed to be 1260 ppm (about 4 times greater than the present). Variation in eccentricity, axial tilt, and precession of the Earth's orbit (regarded as orbital forcing) is fixed at present values. We also use the present value for solar insolation. From the model output for data such as temperature and precipitation, we reconstructed Köppen (Peel et al., 2007) climate classification maps of Madagascar, both at 66 Ma and today. These reconstructions allow us to characterize the climates of Madagascar at 66 Ma and today using widely recognized descriptors, and to compare both with other regions.

Our third experiment repeated the first two experiments, but replaced Madagascar's present day climate for the year 2008 with data for the year 1990. We undertook this experiment because of strong evidence that in any single year, Madagascar's climate can be wildly atypical (or unpredictable), not merely with regard to its seasonal variation but also total rainfall (Dewar and Richard, 2007). Thus, we built our models using years with very different weather patterns, to test how variation in weather today affects our modeling results. Finally, we combined the data for 1990 and 2008 to produce a new Köppen simulation for 66 Ma, and compared this to the combined-year simulation of present conditions.

3. Results

3.1. Overall

At 66 Ma, the simulated Madagascar climate was milder, and generally less seasonal, than it is today. Parts of the island, particularly those in the northwest, were similar to today, but large areas were quite different (Fig. 1). The extreme contrast in habitats today, from the rain forests of the east (with all 12 months experiencing an average precipitation >60 mm) to the arid or semi-arid spiny bush and succulent woodlands of the south and southwest, did not exist at the end of the Cretaceous. Only parts of the eastern coast and isolated areas in the north experienced pronounced dry seasons. Most of Madagascar, including regions that are now very arid with pronounced seasonality, experienced a subtropical mild or mesothermal climate, with dry winters but less seasonal contrast between the austral summer and winter.

3.2. Temperature

At 66 Ma, Madagascar was far south of its current location; consequently, the island was cooler than it is today (Fig. 2). However, the

Please cite this article as: Ohba, M., et al., Madagascar's climate at the K/P boundary and its impact on the island's biotic suite, Palaeogeogr. Palaeoclimatol. Palaeoecol. (2015), http://dx.doi.org/10.1016/j.palaeo.2015.10.028

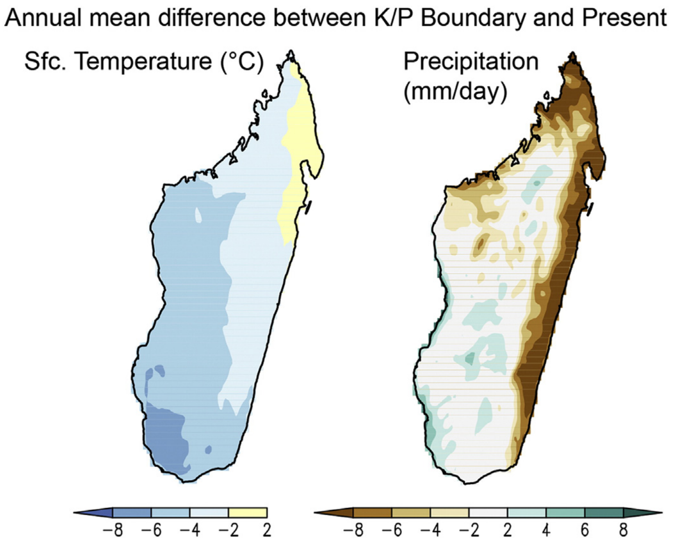

Fig. 1. Differences in annual mean surface temperature (°C) and daily precipitation (mm) (i.e., K/P boundary *minus* today). Mean surface temperature and daily precipitation values for the K/P boundary were generated through our second experiment (2008 simulation).

temperatures displayed in our 66 Ma simulation are in many places only a few degrees lower than those of today (by −0.5 to −8.0 °C, depending on month and location). Given its more southerly position, Madagascar might have been considerably colder if it were not for the very high-atmospheric CO_2, due to heavy volcanic activity. The Deccan volcanic traps in western and central India (Keller et al., 2008) began forming prior to the asteroid impact at the K/P boundary (Bhattacharji et al., 1996; Schoene et al., 2015), although there is recent evidence that the Chicxulub impact itself triggered the largest volcanic eruptions (Richards et al., 2015). Deccan trap volcanism may have lasted 750,000 years, continuing well into the Paleocene, and altering atmospheric chemistry by releasing sulphur dioxide and other volcanic gases over a prolonged period of time (Schoene et al., 2015).

3.3. Rainfall

Our paleoclimate simulation shows no uniform difference in rainfall across Madagascar from 66 Ma to today. Madagascar was generally dry but contained distinctly humid areas (Fig. 3). The zonal contrast (or precipitation difference from east to west) was low, so the intrusion of easterly trade winds was likely weak. The oceans were less aerated than today, and there were likely fewer tropical cyclones. Because of the dominant wind direction, large areas that are extremely dry today (i.e., the south and southwest) were appreciably wetter. However, large areas that are very wet today (i.e., eastern rain forests, Masoala, Sambirano) would then have been significantly drier. The lowland eastern rain forests did not exist. In general, the west was wetter than it is today (influenced by the mid-latitude westerlies and the reduced foehn corresponding with the trade easterlies), and the east was much drier. In the current climate simulation, landfall of tropical cyclones occurs especially in the northeast. But at 66 Ma, tropical cyclones affecting the region would have been much less frequent due the region sitting largely south of the tropical belt.

3.4. Seasonality

Madagascar today has a cold dry winter (roughly April through September) and hot wet summer (roughly October through March). The wettest months (January through March) are also the hottest; driest months (July and August) are also the coldest (Fig. 4; Suppl. Fig. 2).

At the end of the Cretaceous, Madagascar did not experience the current rainfall extremes. The wettest months were drier, especially along the west and east coasts, and the driest months were wetter, especially along the west coast. Exceptions are along the east coast which was consistently drier throughout the year, although least so in April, May and June, which were quite similar in the past to these months today.

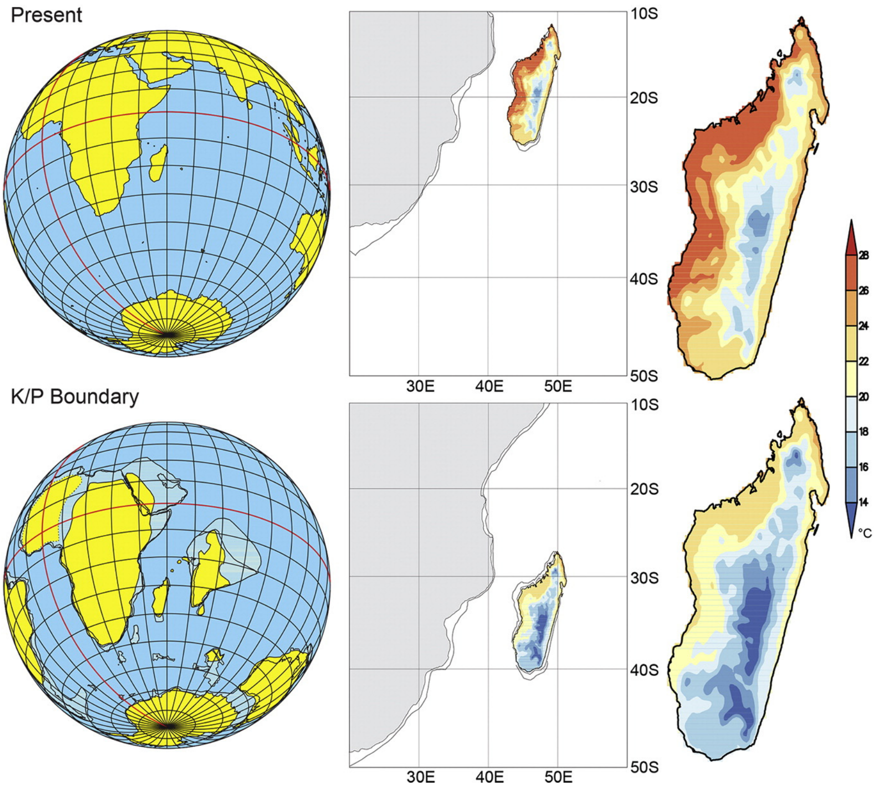

Fig. 2. Position of Madagascar and mean annual surface temperature (°C) at present and at the K/P boundary, the latter generated through our second experiment (2008 simulation).

Please cite this article as: Ohba, M., et al., Madagascar's climate at the K/P boundary and its impact on the island's biotic suite, Palaeogeogr. Palaeoclimatol. Palaeoecol. (2015), http://dx.doi.org/10.1016/j.palaeo.2015.10.028

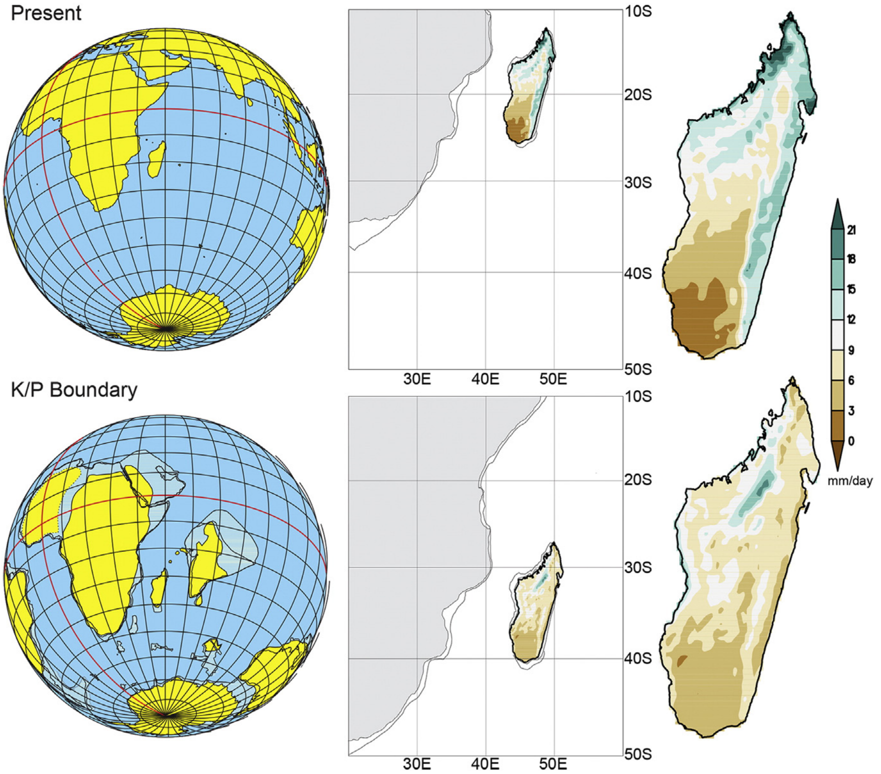

Fig. 3. Position of Madagascar and mean daily precipitation (mm) today and at the K/P boundary, the latter generated through our second experiment (2008 simulation).

In general, the hottest months experienced the smallest reduction in temperature, and the coldest months experienced the greatest drop, particularly in the central highlands and the south. The southwest experienced relatively larger temperature drops than other parts of Madagascar throughout the year. Our model also revealed that continental East Africa (the coastal regions closest to Madagascar) was also colder and generally drier than it is today due to its more southern location.

3.5. Köppen map reconstruction

Our Köppen climate map reconstruction illustrates how very different the climate of Madagascar was 66 Ma as compared to today. The extreme habitats (BS = dry, semi-arid, as exists today in southern and southwestern Madagascar and Af = tropical rain forest with no dry season, as exists today in eastern Madagascar) were not present (Fig. 5). At the K/P boundary, most of Madagascar experienced a subtropical mild or mesothermal climate with moderate humidity but with a dry winter ("Cw" classification). The Köppen map also shows that only small portions of Madagascar could have been characterized as very arid. However, monsoon rain forests existed in the northwest, as they do today.

3.6. Model validation

Our reconstructions of rainfall and surface temperature for Madagascar at the K/P boundary were similar regardless of whether they were "referenced" using modern climate data from 1990 or 2008 (Suppl. Fig. 3). In general, our third experiment (repeating the first two but with 1990 climate data representing modern climate conditions) offers excellent validation of our original paleoclimatological model for the K/P boundary. As a consequence of the tropical cyclones being less frequent in 1990 than in 2008 (Fitchett and Grab, 2014) the simulated climate at 66 Ma based on 1990 data shows slightly weaker precipitation in northern and eastern Madagascar. The annual maximum daily temperature and precipitation maps, however, are nearly identical. Our Köppen maps are less similar. Combining the 1990 and 2008 data reduces the "Cw" (moderate climate, dry winter) area at the K/P boundary but increases the "Am" (tropical mild climate) and "Cf" (moderate climate, no dry season) areas and introduces some "Af" (wet climate, no dry season) patches. The two simulations differ in a parallel fashion to present conditions, however. Both simulations of the K/P boundary show considerably more "Cw" and much less "Aw" habitat at the K/P boundary than at present, and no "BS" (semi-arid) habitat at 66 Ma.

4. Discussion

4.1. Geology and paleoecology as tests of our model reconstruction for the Late Cretaceous

Our first task is to determine how well our model accounts for known depositional environments of the appropriate time period. Less than 50 km southeast of the coastal city of Mahajanga is the famed fossil site Berivotra, where a spectacular Late Cretaceous fauna has been found. The Upper Cretaceous fossils are terrestrial and derive from the Maevarano Formation (including the Masorobe and the Anembalemba members) which has been reconstructed as Maastrichtian in age (72–66 Ma; Suppl. Table 1) (Rogers et al., 2000, 2013). The paleoclimate of Berivotra during the several million years prior to the K/P boundary has been independently reconstructed using the standard tools of sedimentary geology and paleosol lithology (e.g., Stefanovi and Olmstead, 2005; Ocampo and Columbus, 2010; Arakaki et al., 2011; Crottini et al., 2012). The terrestrial fossils and their contexts provide direct evidence that can be compared to inferences drawn from our climate model.

According to our paleoclimatological simulation, considering all of Madagascar, the northwest (including the entire Mahajanga basin region) experienced some of the smallest differences in climate from 66 Ma to today. Indeed, our Köppen classification of the northwest ("Am," meaning tropical monsoon, i.e., a tropical climate that is

Please cite this article as: Ohba, M., et al., Madagascar's climate at the K/P boundary and its impact on the island's biotic suite, Palaeogeogr. Palaeoclimatol. Palaeoecol. (2015), http://dx.doi.org/10.1016/j.palaeo.2015.10.028

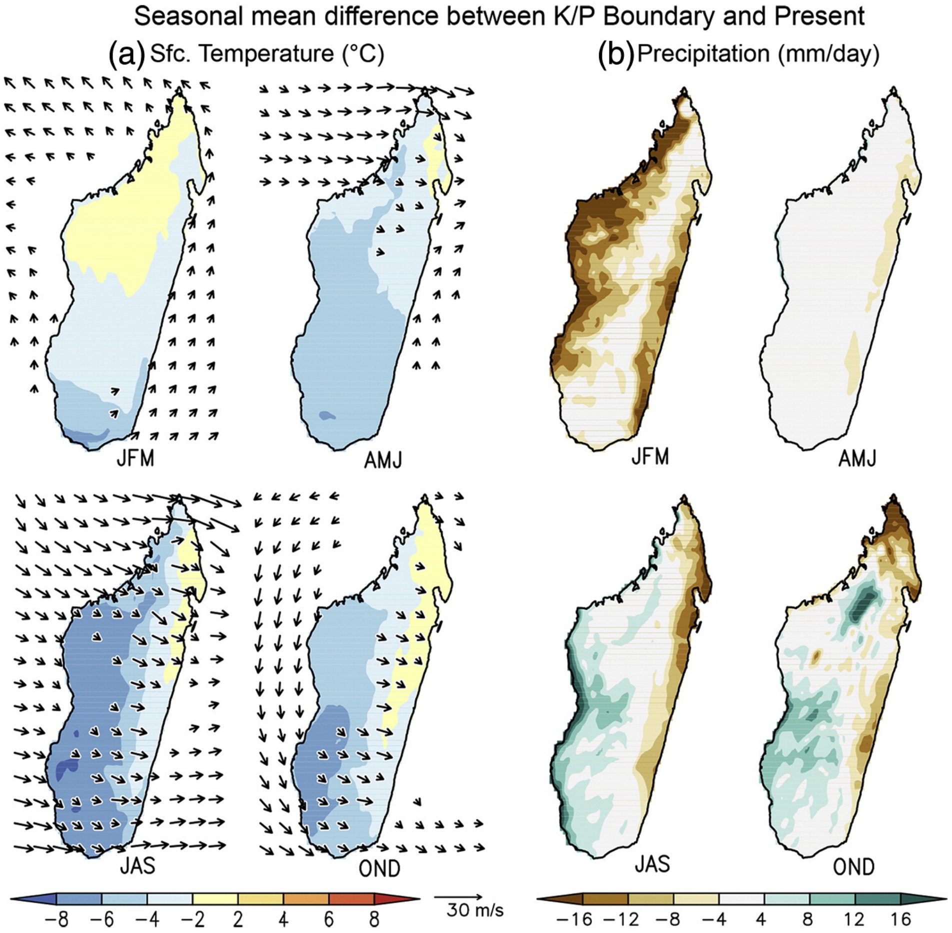

Fig. 4. Seasonal differences (K/P boundary *minus* today) in surface temperature (a) and rainfall (b), as generated by our second experiment. JFM = January through March, AMJ = April through June, JAS = July through September, OND = October through December. Color key indicates the magnitude of the differences.

relatively hot year-round, and that experiences seasonal changes in rainfall due to changes in wind direction) is the same 66 Ma as it is today (Fig. 5). In this region, according to our reconstruction, the temperature at 66 Ma was on average 2–4 °C cooler than today, and the rainfall was on average ~2 mm/day less than today. Rainfall was highly seasonal, as it is today. During January, February, and March, northwestern Madagascar was drier than it is today, but temperatures were not very different. From April to December, rainfall was similar to the present, but temperatures were lower. Today, the Mahajanga basin region receives around 1500 mm of rain per year; we estimate that at 66 Ma the amount would have been 750–800 mm.

On the basis of geological data, Krause and Kley (2010) also surmised that the paleoclimate of Berivotra was not very different from today; i.e., semi-arid but highly seasonal, with cyclones during the wettest months. Distinct wet and dry seasons are inferred from fossils buried in variable stream discharge regimes (Rogers, 2005; Rogers et al., 2007). Such a view is also supported by studies of oxidized calcareous paleosols with carbonate nodules (Rogers et al., 2007). Geochemical and X-ray diffraction analyses of the paleosols from part of the Masorobe formation (Kast et al., 2008), together with “climofunctions” established by (Sheldon et al., 2002), suggest an annual rainfall of between 430 and 1100 mm. This closely matches the rainfall estimates for 66 Ma derived from our model.

The fossil fauna itself provides additional evidence that the northwest was dry but with high seasonality, including sometimes torrential rainfall. One of the vertebrates from the Anembalemba member of the Maevarano formation (a big-headed side-necked turtle called *Erymnochelys*, Podocnemidae) is still extant in Madagascar. It is restricted today to the dry lowlands of western Madagascar, from the Mangoky River in the south to the Sambirano in the north (Gaffney and Forster, 2003). There was a spinicaudatan crustacean (*Ethmosestheria mahajangaensis*), also from the Anembalemba Member of the Maevarano Formation, which lived in temporary pools within what was then a channel-belt system (Stigall and Hartman, 2008). Importantly, the arthropods' fossilized carapaces reveal desiccation structures which suggest seasonal drying of the pools in which they lived. In general, our paleoclimate simulation for the K/P boundary matches expectations derived from the uppermost Cretaceous Berivotra deposits.

4.2. Was Madagascar uniformly arid during the early Paleogene?

The earliest Cenozoic site on Madagascar yielding terrestrial fossils is a Miocene nearshore marine locality (Ramihangihajason et al., 2014); no terrestrial Paleogene sites are known. Nevertheless, we can infer the presence of clades of plants and animals during the Paleogene using a variety of tools including molecular biology, biogeography, and cladistics (Yoder and Nowak, 2006; Crottini et al., 2012; Samonds et al., 2012, 2013; Buerki et al., 2013). There is now strong evidence that much of the spiny thicket flora is young; taxa limited to this habitat originate from the Eocene–Oligocene boundary or later (Buerki et al., 2013). This includes the renowned “octopus trees,” or Didiereoidea, the Malagasy subclade of the Didiereaceae. The Didiereoidea has a clade age less than 20 Ma, perhaps even 15 Ma (Ocampo and Columbus, 2010; Arakaki et al., 2011).

Plants with Mesozoic or early Paleogene clade-origin ages include possible Gondwanan relicts that thrive in dry habitats (e.g., *Hazomalania* Stiassny, 2002 and *Humbertia* Stefanovi and Olmstead, 2005) but also many others that are adapted to humid or sub-humid environments,

Please cite this article as: Ohba, M., et al., Madagascar's climate at the K/P boundary and its impact on the island's biotic suite, Palaeogeogr. Palaeoclimatol. Palaeoecol. (2015), http://dx.doi.org/10.1016/j.palaeo.2015.10.028

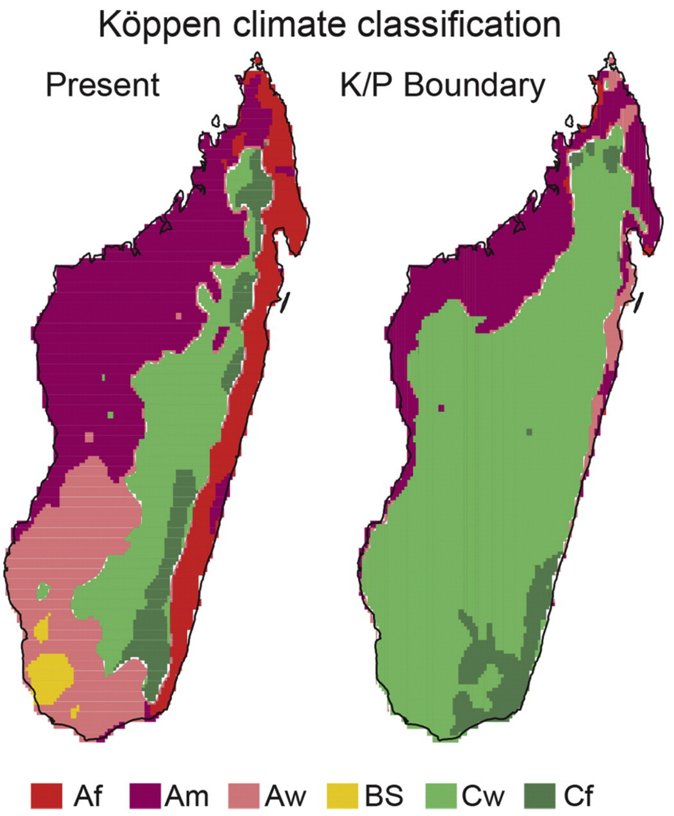

Fig. 5. Köppen climate classification maps. On the left is a Köppen climate map that describes today's climate based on 2008 weather data. On the right is a reconstruction of the climate of Madagascar at the K/P boundary generated by our second experiment (2008 simulation). Af = tropical climate, no dry season; Am = tropical climate, mild; Aw = tropical climate, dry winter; BS = dry climate, semi-arid; Cw = hot moderate climate, dry winter; Cf = hot moderate climate, no dry season.

such as *Didymeles*, an ancient evergreen dioecious tree limited to the eastern Madagascar today (Schatz, 1996; von Balthazar et al., 2003; Anderson et al., 2005; Proches and Ramdhani, 2012); the Diegodendronaceae (Stevens, 2015); *Takhtajania perrieri* (Marquínez et al., 2009); *Dilobeia* (Buerki et al., 2013); the Sarcolaenaceae (Davies et al., 2004; Ducousso et al., 2004); and the Sphaerosepalaceae (Davies et al., 2004). Plant taxa adapted to wet forest habitats outnumber those limited to dry forests and spiny thickets. Wells (2003) inference that Madagascar's Paleogene flora was largely spiny bush was bolstered by the assumption that % endemicity should reflect clade age. This does not hold; the spiny bush of the arid south may have high floral endemicity, but the ancestors of many of its endemic taxa arrived *after* the Eocene, <34 Ma.

Vertebrate clades unknown from Berivotra but inferred to have been present on Madagascar prior to the end of the Eocene are listed in Suppl. Table 2. This table also provides presence/absence data for these clades in three major habitats on Madagascar today (spiny thicket, dry forests, and humid forests). Many of these clades, especially within the amphibians, reptiles, and birds, are represented today everywhere in Madagascar but differ in numbers and densities. Three fish families, Aplocheilidae, Bedotiidae, and Clupeidae, occur only in humid and/or dry forests and not in the spiny thicket (Stiassny, 1990, 2002; Loiselle, 2006); only one family, Milyeringidae, occurs exclusively in the spiny thicket (Sparks and Chakrabarty, 2012).

Some families with strong representation in today's rain forests have apparent basal members adapted to dry forests. This is true of the Mantellidae (frogs), which appear to have radiated during the Eocene (Glaw et al., 2006); Glaw et al. (2006) argue that the most basal clades of each of the three subfamilies of mantellids are adapted to habitats that are drier than those preferred by most members of this family today. Descendants of these basal clades include *Tsingymantis antitra* from the extreme north, which occurs only in seasonal habitats that are moderately dry (Randrianiaina et al., 2011), and which lays its eggs out of water. They also include *Laliostoma labrosum*, the only species that occurs today in the southwest. Some members of the genus *Aglyptodactylus* live in the dry west, but in different habitats (Glaw et al., 1998; Glos and Linsenmair, 2004).

Madagascar has endemic "pelican" or "assassin" spiders (family Archaeidae) that appear to have had an ancient, vicariant origin on the island (Wood et al., 2014). Wood et al. (2014) conducted a phylogenetic analysis with divergence dating; they also reconstructed vegetation types ("rain forest," "deciduous forest," "spiny dry," or "all areas") at every node. Significantly, the basal node at 150 Ma was reconstructed as rain forest, and not a single node older than 50 Ma was reconstructed as "spiny dry." The great majority of vegetation types for nodes with estimated ages >50 Ma were rain or deciduous forest. The authors invoke montane refuges to explain the survival of pelican spiders through periods, such as the early Paleogene, that are presumed to have been very dry on Madagascar. Similar arguments have been proffered to explain the survival of other wet-loving, ancient taxa on Madagascar (see, for example, Townsend et al., 2009 on *Brookesia* chameleons). Of over two dozen species of *Brookesia* chameleons, only one, *B. brygooi*, is adapted to arid habitats (Raxworthy and Nussbaum, 1995). These observations do not support the conclusion that Madagascar was uniformly arid during the early Paleogene.

4.3. Understanding the sequential appearance of clade synapomorphies in their selective contexts: The case of the lemurs of Madagascar

Lemurs are said to differ from other primates in that many express characteristics (e.g., female dominance, low basal metabolic rate, small day range, small group size, low activity levels, seasonal reproduction, weaning synchrony, seasonal torpor, cathemerality) that are thought to be mechanisms for coping with the energy-poor environments of Madagascar, i.e., limited resource availability, poor soil and fruit quality, cyclones, cold, drought, strong seasonality, and general climatic stochasticity or "unpredictability" (Wright, 1999; Dewar and Richard, 2007). Low activity levels, possibly related to depressed metabolism, can be inferred for the recently extinct giant lemurs as well as still-extant lemurs. The giant lemurs have skeletal traits that reflect slow, deliberate locomotion (Jungers et al., 2002) and other traits that may reflect depressed metabolism and low activity levels (see Walker et al., 2008, on balance, activity levels, and semicircular canals, and Hogg et al., 2015, on low dental Retzius periodicities, which in turn may reflect short Havers–Halberg oscillations; see also Bromage et al., 2012; Houssaye, 2014).

Lemur ancestors likely arrived on Madagascar between 65 Ma and 50 Ma (Poux et al., 2005; Springer et al., 2012; Kistler et al., 2015). Interpreting unusual synapomorphies as adaptations to strong seasonality and general climatic unpredictability makes little sense if, as has been argued on the basis of Wells (2003) climate reconstructions, unpredictable climates only appeared during the late Miocene or Pliocene (with the intensification of Indian Ocean monsoons). However, it is also not at all clear that unusual climatic stochasticity characterized Madagascar at the time of initial lemur colonization (≥50 Ma). Indeed, our models for the K/P boundary argue strongly that this was not the case. There was nothing particularly hostile about the climate of Madagascar during the Late Cretaceous and early Paleogene.

As environmental conditions have changed, sometimes dramatically, over time, synapomorphies can only be understood within the time/space framework in which they appeared. Energy-saving lemur characteristics did not arise at a single point in time and are in fact far from universal among lemurs. *Daubentonia*, for example, ranges widely (Perry et al., 2013) and does not exhibit depressed basal metabolism or other traits associated with energy conservation. In order to understand the adaptive nature of puzzling lemur traits, each must be considered

Please cite this article as: Ohba, M., et al., Madagascar's climate at the K/P boundary and its impact on the island's biotic suite, Palaeogeogr. Palaeoclimatol. Palaeoecol. (2015), http://dx.doi.org/10.1016/j.palaeo.2015.10.028

within the appropriate geological and paleoclimatic context in which it was selected.

Kistler et al. (2015) recently published a molecular phylogeny of lemurs with divergence dates for each of the eight lemur families. Advances in the analysis of ancient DNA allowed their inclusion of extinct as well as extant lemur families. At ~50 Ma, two lineages diverged—that leading to the Daubentoniidae and that leading to all other lemurs. Most of the "unusual" characteristics emerged only in the latter group, which shares (at ~31 Ma, long after the initial colonization of Madagascar by the ancestral lemur) a much more recent common ancestor. Traits that likely appeared at ~31 Ma in the last common ancestor of seven of the eight lemur families include constrained (low) Retzius periodicity, reduced activity levels, and female dominance. At ~23 Ma, facultative seasonal torpor arose in ancestor of Cheirogaleidae (without *Phaner*, which lacks this trait, and which falls outside the clade comprising all other cheirogaleids). At ~20 Ma, flexible activity rhythms including cathemerality arose in the ancestor of Lemuridae. At ~15 Ma, obligate seasonal torpor evolved in ancestor of *Cheirogaleus*. Thus, the "unusual" lemur traits likely evolved between 31 and 15 Ma. It goes without saying that we lack detailed climate reconstructions of Madagascar for this period, but we do know that 31 Ma immediately postdates a time of precipitous global cooling and extinctions at the Eocene/Oligocene boundary (34 Ma). The climate of Madagascar at this time was undoubtedly very different from that encountered by the initial colonizing lemur.

5. Conclusion

Our climate simulation offers support to parts of Wells (2003) climate reconstruction but contradicts others. We concur with Wells (2003) that, during the Late Cretaceous and early Paleogene, Madagascar was more arid than it is today, but this does not apply uniformly across the island. There is no evidence that the spiny bush is the oldest vegetation biome in Madagascar; indeed, it did not exist at the K/P boundary, just as the eastern rain forest was not present. There probably were, however, mesic forests in central Madagascar. Moderate climates with dry winters characterized most of Madagascar. Monsoon or seasonal forests did exist in the northwest, as they do today. Madagascar's spiny bush and eastern rain forest may have arisen simultaneously, after the early Paleogene, as Madagascar drifted northward, and the southwest, shielded from the trade winds by the eastern escarpment, could no longer receive moisture from the westerlies.

According to our reconstruction, an assortment of plant, vertebrate, and invertebrate clades adapted to dry or mesic conditions (or both), should have populated Madagascar in the early Paleogene. Conditions were mildly cooler than today. Such conditions explain the range of taxa known or hypothesized to have existed on Madagascar in the early Paleogene, and obviate the need to posit montane refuges for taxa intolerant of dry conditions. Last, the notion that lemurs evolved energy-saving traits in response to particularly hostile and unpredictable early Paleogene climatic conditions needs to be reconsidered in light of the climate reconstruction presented here.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2015.10.028.

References

Ali, J.R., Aitchison, J.C., 2008. Gondwana to Asia: plate tectonics, paleogeography and the biological connectivity of the Indian sub-continent from the Middle Jurassic through latest Eocene (166–35 Ma). Earth Sci. Rev. 88 (3-4), 145–166.

Ali, J., Krause, D., 2011. Late Cretaceous bioconnections between Indo-Madagascar and Antarctica: refutation of the Gunnerus Ridge causeway hypothesis. J. Biogeogr. 38, 1855–1872.

Anderson, C., Bremer, K., Friis, E., 2005. Dating phylogenetically basal eudicots using rbcL sequences and multiple fossil reference points. Am. J. Bot. 92 (10), 1737–1747.

Arakaki, M., et al., 2011. Contemporaneous and recent radiations of the world's major succulent plant lineages. Proc. Natl. Acad. Sci. U. S. A. 108, 8379–8384.

Bhattacharji, S., Chatterjee, N., Wampler, J., Nayak, P., Deshmukh, S., 1996. Indian intraplate and continental margin rifting, lithospheric extension, and mantle upwelling in Deccan flood basalt volcanism near the K/T boundary: evidence from mafic dike swarms. J. Geol. 104, 379–398.

Bromage, T., Hogg, R., Lacruz, R., Hou, C., 2012. Primate enamel evinces long period biological timing and regulation of life history. J. Theor. Biol. 305, 131–144.

Buerki, S., Devey, D., Callmander, M., Phillipson, P., Forest, F., 2013. Spatio-temporal history of the endemic genera of Madagascar. Bot. J. Linn. Soc. 171 (2), 304–329.

Chand, S., Subrahmanyam, C., 2003. Rifting between India and Madagascar – mechanism and isostasy. Earth Planet. Sci. Lett. 210, 317–332.

Crottini, A., et al., 2012. Vertebrate time-tree elucidates the biogeographic pattern of a major biotic change around the K–T boundary in Madagascar. Proc. Natl. Acad. Sci. U. S. A. 109 (14), 5358–5363.

Davies, T., et al., 2004. Darwin's abominable mystery: insights from a supertree of the angiosperms. Proc. Natl. Acad. Sci. U. S. A. 101 (7), 1904–1909.

de Wit, M., 2003. Madagascar: heads it's a continent, tails it's an island. Annu. Rev. Earth Planet. Sci. 31, 213–248.

Dewar, R., Richard, A., 2007. Evolution in the hypervariable environment of Madagascar. Proc. Natl. Acad. Sci. U. S. A. 104 (34), 13723–13727.

Ducousso, M., et al., 2004. The last common ancestor of Sarcolaenaceae and Asian dipterocarp trees was ectomycorrhizal before the India–Madagascar separation, about 88 million years ago. Mol. Ecol. 13, 231–236.

Emmel, B., Jacobs, J., Kastowski, M., Graser, G., 2006. Phanerozoic upper crustal tectonothermal development of basement rocks from central Madagascar: an integrated fission-track and structural study. Tectonophysics 412, 61–86.

Emmel, B., Boger, S., Jacobs, J., Daszinnies, M., 2012. Maturity of central Madagascar's landscape – low thermochronological constraints. Gondwana Res. 21, 704–713.

Fitchett, J., Grab, S., 2014. A 66-year tropical cyclone record for south-east Africa: temporal trends in a global context. Int. J. Climatol. 34 (13), 3604–3615.

Gaffney, E., Forster, C., 2003. Side-necked turtle lower jaws (Podocnemididae, Bothremydidae) from the Late Cretaceous Maevarano Formation of Madagascar. Am. Mus. Novit. 3397, 1–13.

Glaw, F., Vences, M., Bohme, W., 1998. Systematic revision of the genus *Aglyptodactylus* Boulenger, 1919 (Amphibia: Ranidae), and analysis of its phylogenetic relationships to other Madagascan ranid genera (*Tomopterna*, *Boophis*, *Mantidactylus*, and *Mantella*). J. Zool. Syst. Evol. Res. 36, 17–37.

Glaw, F., Hoegg, S., Vences, M., 2006. Discovery of a new basal relict lineage of Madagascan frogs and its implications for mantellid evolution. Zootaxa 1334, 27–43.

Glos, J., Linsenmair, K., 2004. Descriptions of the tadpoles of *Aglyptodactylus laticeps* and *Aglyptodactylus securifer* from Western Madagascar, with notes on life history and ecology. J. Herpetol. 38 (1), 131–136.

Hogg, R., Godfrey, L., Schwartz, G., Dirks, W., Bromage, T., 2015. Lemur biorhythms and life history evolution. PLoS One 10 (8), e0134210.

Houssaye, A., 2014. Advances in vertebrate palaeohistology: recent progress, discoveries, and new approaches. Biol. J. Linn. Soc. 112 (4), 645–648.

Jungers, W., et al., 2002. Ecomorphology and behavior of giant extinct lemurs from Madagascar. In: Plavcan, J., Kay, R., Jungers, W., van Schaik, C. (Eds.), Reconstructing Behavior in the Primate Fossil Record. Plenum Press, New York, pp. 371–411.

Kast, S., Rogers, R., Curry Rogers, K., 2008. Reconstructing Late Cretaceous climate in the Mahajanga Basin of northwestern Madagascar. J. Vertebr. Paleontol. 28 (Suppl. 3), 99A.

Keller, G., Adatte, T., Gardin, S., Bartolini, A., Bajpai, S., 2008. Main Deccan volcanism phase ends near the K–T boundary: evidence from the Krishna–Godavari Basin, SE India. Earth Planet. Sci. Lett. 268, 293–311.

Kistler, L., et al., 2015. Comparative and population mitogenomic analyses of Madagascar's extinct, giant 'subfossil' lemurs. J. Hum. Evol. Spec. Issue 79 (SI), 45–54.

Koechlin, J., 1972. Flora and fauna of Madagascar. In: Battistini, R., Richard-Vindard, G. (Eds.), Biogeography and Ecology of Madagascar. W. Junk, The Hague.

Krause, D., Kley, N., 2010. *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. *Society of Vertebrate Paleontology Memoir 10*. J. Vertebr. Paleontol. 30 (6), 236.

Kusky, T., Toraman, E., Raharimahefa, T., Rasoazanamparany, C., 2010. Active tectonics of the Alaotra–Ankay Graben System, Madagascar: possible extension of Somalian–African diffusive plate boundary? Gondwana Res. 18, 274–294.

Loiselle, P., 2006. A review of the Malagasy *Pachypanchax* (Teleostei: Cyprinodontiformes, Aplocheilidae) with descriptions of four new species. Zootaxa 1366, 1–44.

Marquínez, X., Lohmann, L., Salatino, M., Salatino, A., González, F., 2009. Generic relationships and dating of lineages in Winteraceae based on nucleuar (ITS) and plastic (rpS16 and psbA-trnH) sequence data. Mol. Phylogenet. Evol. 53, 435–449.

Ocampo, G., Columbus, J., 2010. Molecular phylogenetics of suborder Cactineae (Caryophyllales), including insights into photosynthetic diversification and historical biogeography. Am. J. Bot. 97, 1827–1847.

Ohba, M., Ueda, H., 2010. A GCM Study on effects of continental drift on tropical climate at the Early and Late Cretaceous. J. Meteorol. Soc. Jpn. 88 (6), 869–881.

Onogi, K., et al., 2007. The JRA-25 Reanalysis. J. Meteorol. Soc. Jpn. 85, 369–432.

Peel, M., Finlayson, B., McMahon, T., 2007. Updated world map of the Köppen–Geiger climate classification. Hydrol. Earth Syst. Sci. 11, 1633–1644.

Perry, G., et al., 2013. Aye-aye population genomic analyses highlight an important center of endemism in northern Madagascar. Proc. Natl. Acad. Sci. U. S. A. 110 (15), 5823–5828.

Poux, C., et al., 2005. Asynchronous colonization of Madagascar by the four endemic clades of primates, tenrecs, carnivores, and rodents as inferred from nuclear genes. Syst. Biol. 54 (5), 719–730.

Please cite this article as: Ohba, M., et al., Madagascar's climate at the K/P boundary and its impact on the island's biotic suite, Palaeogeogr. Palaeoclimatol. Palaeoecol. (2015), http://dx.doi.org/10.1016/j.palaeo.2015.10.028

Proches, S., Ramdhani, S., 2012. Analyses towards determining Madagascar's place in global biogeography. Curr. Zool. 58, 363–374.

Ramihangihajason, T., et al., 2014. Miocene foraminifera from Nosy Mahakamby and Amparafaka, Mahajanga Basin, Madagascar. J. Afr. Earth Sci. 100, 409–417.

Randrianiaina, R., Köhler, J., Glos, J., Vences, M., Glaw, F., 2011. Where to grow in the Tsingy? Limestone rock pools as breeding habitats of the relict frog *Tsingymantis antitra* from Madagascar and description of its tadpole. Salamandra 47, 77–89.

Raxworthy, C., Nussbaum, R., 1995. Systematics, speciation and biogeography of the dwarf chameleon (*Brookesia*; Reptilia, Squamata, Chamaeleontidae) of northern Madagascar. J. Zool. Soc. Lond. 235, 525–558.

Richards, M.A., et al., 2015. Triggering of the largest Deccan eruptions by the Chicxulub impact. Geol. Soc. Am. Bull. http://dx.doi.org/10.1130/B31167.1.

Rogers, R., 2005. Fine-grained debris flow and extraordinary vertebrate burials in the Late Cretaceous of Madagascar. Geology 33 (4), 297–300.

Rogers, R.R., Hartman, J.H., Krause, D.W., 2000. Stratigraphic analysis of Upper Cretaceous rocks in the Mahajanga Basin, northwestern Madagascar: implications for ancient and modern faunas. J. Geol. 108, 275–301.

Rogers, R., Krause, D., Curry Rogers, K., Rasoamiaramanana, A., Rarahantarisoa, L., 2007. Paleoenvironment and paleoecology of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. J. Vertebr. Paleontol. 27 (Supplement 2), 21–31 (Memoir Memoir 8).

Rogers, R., et al., 2013. A new, richly fossiliferous member comprised of tidal deposits in the Upper Cretaceous Maevarano Formation, northwestern Madagascar. Cretac. Res. 44, 12–29.

Samonds, K., et al., 2012. Spatial and temporal arrival patterns of Madagascar's vertebrate fauna explained by distance, ocean currents, and ancestor type. Proc. Natl. Acad. Sci. U. S. A. 109, 5352–5357.

Samonds, K., et al., 2013. Imperfect isolation: factors and filters shaping Madagascar's extant vertebrate fauna. PLoS One 8 (4), e62086.

Schatz, G., 1996. Malagasy/Indo-Australo-Malesian phytogeographic connections. In: Lourenço, W. (Ed.), Biogéographie de Madagascar. ORSTOM, Paris, pp. 73–83.

Schettino, A., Scotese, C.R., 2005. Apparent polar wander paths for the major continents (200 Ma to the present day): a palaeomagnetic reference frame for global plate tectonic reconstructions. Geophys. J. Int. 163 (2), 727–759.

Schoene, B., et al., 2015. U-Pb geochronology of the Deccan Traps and relation to the end-Cretaceous mass extinction. Science 347 (6218), 182–184.

Sheldon, N., Retallack, G., Tanaka, S., 2002. Geochemical climofunctions from North American soils and application to paleosols across the Eocene–Oligocene boundary in Oregon. J. Geol. 110, 687–696.

Smith, A.G., Smith, D.G., Funnell, B.M., 1994. Atlas of Mesozoic and Cenozoic coastlines.

Sparks, J., Chakrabarty, P., 2012. Revision of the endemic Malagasy cavefish genus *Typhleotris* (Teleostei, Gobiiformes, Milyeringidae), with discussion of its phylogenetic placement and description of a new species. Am. Mus. Novit. 3764, 1–28.

Springer, M., et al., 2012. Macroevolutionary dynamics and historical biogeography of primate diversification inferred from a species supermatrix. PLoS One 7 (11), e49521.

Stefanovi, S., Olmstead, R., 2005. Down the slippery slope: plastid genome evolution in Convolvulaceae. J. Mol. Evol. 61, 292–305.

Stevens, P., 2015. Angiosperm Phylogeny Website. Version 12 (July 2012).

Stiassny, M., 1990. Notes on the anatomy and relationships of the Bedotiid fishes of Madagascar, with a taxonomic revision of the genus *Rheocles* (Atherinomorpha: Bedotiidae). Am. Mus. Novit. 2979, 1–33.

Stiassny, M.L.J., 2002. Revision of *Sauvagella* Bertin (Clupeidae; Pellonulinae; Ehiravini) with a description of a new species from the freshwaters of Madagascar and diagnosis of the Ehiravini. Copeia 1, 67–76.

Stigall, A., Hartman, J., 2008. A new spinicaudatan genus (Crustacea: “Conchostraca”) from the Late Cretaceous of Madagascar. Paleontology 51 (5), 1053–1067.

Torsvik, T., Smethurst, M., 1999. Plate tectonic modelling: virtual reality with GMAP. Comput. Geosci. 25, 395–402.

Townsend, T., Vieites, D., Glaw, F., Vences, M., 2009. Testing species-level diversification hypotheses in Madagascar: the case of microendemic *Brookesia* leaf chameleons. Syst. Biol. 58 (6), 641–656.

von Balthazar, M., Schatz, G., Endress, P., 2003. Female flowers and inflorescences of Didymelaceae. Plant Syst. Evol. 237, 199–208.

Walker, A., Ryan, T., Silcox, M., Simons, E., Spoor, F., 2008. The semicircular canal system and locomotion: the case of extinct lemuroids and lorisoids. Evol. Anthropol. 17 (3), 135–145.

Wells, N., 2003. Some hypotheses on the Mesozoic and Cenozoic paleoenvironmental history of Madagascar. In: Goodman, S., Benstead, J. (Eds.), The Natural History of Madagasc,. The University of Chicago Press, Chicago, IL, pp. 16–34.

Wood, H., Gillespie, R., Griswols, C., Wainwright, P., 2014. Why is Madagascar special? The extraordinarily slow evolution of pelican spiders (Araneae, Archaeidae). Int. J. Organ. Evol. 69 (2), 462–481.

Wright, P., 1999. Lemur traits and Madagascar ecology: coping with an island environment. Yearbook Phys. Anthropol. 42, 31–72.

Yoder, A.D., Nowak, M.D., 2006. Has vicariance or dispersal been the predominant force in Madagascar? Only time will tell. Annu. Rev. Ecol. Syst. 37, 405–431.

Please cite this article as: Ohba, M., et al., Madagascar's climate at the K/P boundary and its impact on the island's biotic suite, Palaeogeogr. Palaeoclimatol. Palaeoecol. (2015), http://dx.doi.org/10.1016/j.palaeo.2015.10.028