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Seasonal migration of marsupial megafauna in Pleistocene Sahul (Australia–New Guinea)

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Seasonal two-way migration is an ecological phenomenon observed in a wide range of large-bodied placental mammals, but is conspicuously absent in all modern marsupials. Most extant marsupials are typically smaller in body size in comparison to their migratory placental cousins, possibly limiting their potential to undertake long-distance seasonal migrations. But what about earlier, now-extinct giant marsupial megafauna? Here we present new geochemical analyses which show that the largest of the extinct marsupial herbivores, the enormous wombat-like *Diprotodon optatum*, undertook seasonal, two-way latitudinal migration in eastern Sahul (Pleistocene Australia–New Guinea). Our data infer that this giant marsupial had the potential to perform round-trip journeys of as much as 200 km annually, which is reminiscent of modern East African mammal migrations. These findings provide, to our knowledge, the first evidence for repetitive seasonal migration in any metatherian (including marsupials), living or extinct, and point to an ecological phenomenon absent from the continent since the Late Pleistocene.

1. Introduction

Sahul (Pleistocene Australia–New Guinea) was once a continent brimming with giant marsupials. Collectively referred to as the ‘megafauna’, these behemoths included a wide range of oversized kangaroos, wombats, marsupial ‘lions’, ‘rhinos’ and ‘tapirs’. With their earliest origins dating back to at least the Late Oligocene, such taxa attained their largest-ever body sizes by the Late Pleistocene, a time that culminated in their continental extinction [1]. Hypotheses developed to explain the cause(s) of the die-off of Sahul’s Late Pleistocene megafauna are most commonly tested using geochronology: if the extinctions can be shown to coincide with earliest human colonization or episodes of intense climate change, the potential driving mechanisms may be inferred on the basis of such temporal relationships [2,3].

Thus, testing of the major extinction hypotheses has become heavily reliant on comprehensive geochronological datasets of humans, climate change and megafaunal occurrences in time (and space). For the megafauna of Sahul at least, it is a dataset that at present can be described only as patchy. Few of the extinct Sahulian species have reliable ages, with the majority lacking dating of any kind [4,5]. Moreover, the focus on using only geochronology

to test the dominant extinction hypotheses ignores critical biological and ecological factors that may have played a role in the extinctions.

The giant wombat-like *Diprotodon optatum* was a key member of the megafaunal herbivore guild of Pleistocene Australia [3]. Standing 1.8 m at the shoulder, and weighing nearly 3000 kg, it was the largest marsupial ever to exist [6]. With a near continent-wide distribution, the monotypic *Diprotodon* was the last surviving member of the Diprotodontidae, a diverse superfamily of mega-marsupials that roamed Sahul for more than 24 Myr. *Diprotodon* has been interpreted as a selective browser, possibly consuming leaves and woody materials [7–9]. Other than being sexually dimorphic [10], the life-history traits of *Diprotodon* are poorly known and its ecological role in Australia has remained unclear.

The paucity of palaeobiological and palaeoecological information about *Diprotodon* and other Sahulian Pleistocene megafauna has limited the testing of leading hypotheses about their extinction. To address this, we here report new geochemical data from an upper incisor of *Diprotodon*. Stable isotope analyses of tooth enamel can provide great insights into life habits of extinct taxa [11]. Unlike bone collagen, tooth enamel is ideal for palaeoecological and palaeobiological analyses as the biogenic isotope signatures are not easily remodelled after its formation [12]. Analyses of $\delta^{13}\text{C}$ reveal dietary information, specifically whether an organism fed on plants that use the C_3 or C_4 photosynthetic pathways [11]. In modern Australia, C_3 plants typically include grasses, shrubs and trees, whereas C_4 plants, with few exceptions (e.g. arid-adapted saltbushes) [13], are dominantly grasses [14]. $\delta^{18}\text{O}$ isotopes reflect water intake, and along with $\delta^{13}\text{C}$, provide a proxy for past climatic conditions [11]. Strontium isotope ratios ($^{87}\text{Sr}/^{86}\text{Sr}$) reflect local geology as Sr is incorporated into organic tissues, including teeth, from water and food [15]. As different regions may have different local Sr isotope ratios, fluctuation of those ratios through an ever-growing tooth may reflect an organism's feeding activities across distinct geologic provinces during its lifetime [15].

Diprotodon had ever-growing (euhiposodont) incisors that were constantly worn down on the occlusal tip as a result of feeding activities. By analysing a serial-sampled incisor (figure 1; electronic supplementary material, 3D model 1), we were able to map both diet and geographical movement of a *Diprotodon* individual throughout the last years of its life, thus providing new insights into its palaeoecology and palaeobiology.

2. Material and methods

(a) Sampling

Geochemical sampling focused on an upper incisor of *D. optatum* collected from the Darling Downs, southeastern Queensland, Australia (Queensland Museum Fossil (QMF) 3452; electronic supplementary material, figure S1, 3D model 1). The specimen was selected because it is mostly complete, with well preserved and intact enamel along its length. The enamel is confined to the dorsal and external lateral surface of the tooth. Powdered enamel samples were collected for C, O and Sr isotope, and trace-element (including rare earth elements; REE), analyses and powdered dentine samples for dating, all using a low-speed electric drill and carbide burs. Stable C and O samples were drilled at 1–2 mm intervals, and Sr isotope and trace-

Figure 1. Anterior portion of *Diprotodon* incisor demonstrating serial-sampling of enamel. The tooth (total length approximately 300 mm as measured along its dorsal surface) is accessioned in the collection of the Queensland Museum (QMF3452). See the electronic supplementary material, 3D model 1 for an interactive 3D model of the complete tooth. (Online version in colour.)

element samples were collected at approximately 7 mm intervals, for the entire length of the tooth (figure 1; electronic supplementary material, 3D model 1). Dentine samples were collected at approximately 2 mm intervals from two cross sections through the tooth using a microsampling procedure [16].

(b) Geochronology

Dentine samples were dated with uranium–thorium (U–Th) methods (see the electronic supplementary material, text). The analyses were conducted using a Nu Plasma HR multi-collector inductively coupled plasma-mass spectrometer at the Radiogenic Isotope Facility (RIF), The University of Queensland (UQ).

(c) Isotope and trace-element geochemistry

For C and O isotopes, samples of powdered enamel were chemically treated using 30% H_2O_2 and 0.1 N acetic acid to remove organics for analyses of stable isotopes of carbon and oxygen. Samples were measured using a ThermoFinnigan DeltaPlus XP mass spectrometer at the University of Rochester Stable Isotope Ratios in the Environment Analytical Laboratory (SIREAL). C and O isotopes are reported in permil (‰) and standardized to Vienna Pee-Dee Belemnite (V-PDB).

Powdered samples for Sr isotope and trace-element analysis were digested in double-distilled nitric acid, with any trace organics decomposed of using a few drops of H_2O_2 . Each sample solution was then split into two aliquots for separate Sr isotope and trace-element measurements. Trace-element concentrations were measured on a Thermo X-series II inductively coupled plasma-mass spectrometer in the RIF at UQ, with the resulting data normalized to MuQ (Mud of Queensland) for interpretation following [17]. After column chemistry separation using Eichrom Sr-spec resin, Sr isotope compositions were measured using a VG Sector-54 thermal ionization mass spectrometer in the RIF at UQ.

(d) Migration analysis

Periodicity was determined with spectral analysis using the REDFIT procedure [18] implemented in PAST v. 2.17c [19]. The highest oversampling (four) was selected in order to increase the number of points through the spectral analysis. Periodicity in the data was tested against a null hypothesis of red noise,

Figure 2. Bivariate plot of carbon (C) and oxygen (O) for teeth of *Diprotodon* and modern kangaroos (*Macropus*). $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values for kangaroos grouped by their climatic region. Labels on axes indicate the boundary between a C_3 -dominated, C_3/C_4 mixed and C_4 -dominated diets. Data for modern kangaroos from Murphy & Bowman [23].

with a first-order autoregressive (AR1) process considered sufficient to explain a red-noise signature [20]. Only points possessing power above the 90% false alarm level (calculated through Monte Carlo simulation) were selected [21] and included in the subsequent sinusoidal regression.

3. Results

(a) Age of specimen

We obtained 24 U–Th ages directly from dentine in the tooth (see the electronic supplementary material, text and table S1). The results suggest that the individual lived around 300 ka (kiloannum), and at a time coinciding with a more humid climate in central eastern Sahul than today (e.g. [22]).

(b) Trace elements

Trace-element (including REE) concentrations were measured on powdered enamel samples ($n = 39$) collected over the length of the incisor to monitor post-depositional (diagenetic) uptake of elements. REE concentrations along the incisor are consistent with some diagenetic trace-element uptake (see the electronic supplementary material text and table S2). Correlation of a slight elevation in Sr concentration towards the posterior (younger) end of the incisor with REE concentration allowed correction for the diagenetic effect on $^{87}\text{Sr}/^{86}\text{Sr}$ ratio values (electronic supplementary material, table S3) from the most altered portion of the tooth using a simple mixing calculation (see the electronic supplementary material, text).

(c) Carbon and oxygen isotopes

The $\delta^{13}\text{C}$ values ($n = 79$) along the incisor range between -5‰ and -8.9‰ (electronic supplementary material, table S4) suggesting a mixed herbivorous diet of both C_3 and C_4 vegetation for our individual (figure 2). This finding is consistent with morphology- [7,8], geochemical-, and

microwear [9] dietary interpretations. The $\delta^{18}\text{O}$ values ($n = 78$) range from -6.4‰ to 1.9‰ (electronic supplementary material, table S4), corresponding to $\delta^{18}\text{O}$ values of teeth in modern tropical marsupials (figure 2). This interpretation is supported by palaeontological evidence of extensive tropical rainforest in central eastern Sahul during the Middle Pleistocene [22], unlike the temperate to sub-tropical climate of the modern Darling Downs.

(d) Strontium isotopes and migration analysis

The $^{87}\text{Sr}/^{86}\text{Sr}$ ratios ($n = 37$) fluctuate between 0.706333 and 0.707396 along the tooth (electronic supplementary material, table S3). Despite minor diagenetic alteration, a REDFIT spectral analysis demonstrates clear periodicity in $^{87}\text{Sr}/^{86}\text{Sr}$ along the incisor with four periods being significantly different from background noise (figure 3a; electronic supplementary material, text). Of these, only the first three frequencies, corresponding to periods of 95.92, 50.05 and 33.86 mm along the tooth, produced significant sinusoidal regressions. Cumulative sinusoids constructed using all possible combinations of summed periods consistently produced higher Akaike information criterion values than single period sinusoidal curves, and were therefore not considered further. When the three periods were used in sinusoidal regressions, only the first period, equivalent to a period of 95.92 mm along the tooth, produced significant regressions in the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ profiles (figure 3b–d). This period explains 21.4% of the $\delta^{13}\text{C}$ variance ($p < 0.001$) and 6.9% of the $\delta^{18}\text{O}$ variance ($p = 0.048$) in sinusoidal regressions. To explore diagenetic influences on the biogenic signatures, we tested for cyclicity in total REE and Sr concentrations using the Sr isotope sinusoidal regression, but did not find a significant correlation ($p = 0.14$ and $p = 0.81$, respectively). Thus, apart from the most posterior end of the tooth, the fossilization process did not significantly disrupt original biogenic signatures,

Figure 3. REDFIT spectral analysis of the transformed Sr isotope data (a), and sinusoidal regression of the strontium (b), carbon (c) and oxygen (d) isotope profiles. For the REDFIT analysis, the raw isotope data were transformed by removing the linear trend through subtraction of a linear regression line of tooth position and isotope value. Use of untransformed values did not alter the findings. The four frequencies significantly different from background noise and used in the subsequent sinusoidal regressions are illustrated. The period for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ regressions was based on the best performing sinusoidal regression using the periods determined from the REDFIT analysis of the Sr isotopic profile (best Sr model shown). Model selection was made on the basis of Akaike information criterion (AIC), and where $\Delta\text{AIC} < 2$, by the amount of variance explained by the model.

thus, showing that the palaeobiological signals preserved in the tooth are true to life.

4. Discussion

Our findings provide previously unknown insights into the palaeobiology and palaeoecology of *Diprotodon*. The Sr isotope data clearly suggest that the individual travelled cyclically, revisiting the same geologic provinces several times over the time of incisor growth. The data do not support nomadism wherein more irregular movement patterns would be expected; rather, the pattern is that of a ‘two worlds’, or round-trip, migration [24] with similar paths on both legs of the journey. Furthermore, the significant relationship of the Sr isotope, $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ cycles provides compelling evidence that migration, diet and water intake

were intimately linked, suggesting seasonal migration to optimize food and water intake through the year.

If the cycles are indeed annual, the *Diprotodon* tooth represents approximately 2 years and 11 months of growth, or a growth rate of $0.2\text{--}0.3\text{ mm d}^{-1}$ on average. That rate is consistent with a wide range of growth rates of living mammals that have ever-growing incisors such as porcupines (0.2 mm d^{-1}) [25], Indian elephants (0.4 mm d^{-1}) [25], and importantly, wombats (up to 0.2 mm d^{-1}) [26], the closest living relative of *Diprotodon*.

The Darling Downs *Diprotodon* individual appears to have had a relatively restricted diet, with $\delta^{13}\text{C}$ values varying by only 3.9‰ through the seasons, a finding that is also consistent with individuals from elsewhere [9]. By contrast, modern wombats in southeastern Australia vary by as much as 9‰ between maximum (summer) and minimum (winter) $\delta^{13}\text{C}$ values [26]. Hence: (i) *Diprotodon* may have

Figure 4. Map indicating location of Darling Downs in central eastern Australia. High topographic relief in the region is provided by the bordering Great Dividing Range. The Condamine River is the major drainage basin that flows northwest through the Darling Downs. Numbers represent $^{87}\text{Sr}/^{86}\text{Sr}$ isotopic ratios of local bedrock, sediments and groundwater (following [27–30]). (Online version in colour.)

had a more selective diet than modern wombats; (ii) there was less seasonality (and less variation in available food) in the Darling Downs during the Pleistocene; and/or (iii) migration allowed *Diprotodon* to track its preferred food mix across multiple landscapes through the seasons. If the last hypothesis is true, then migration in *Diprotodon* may have been an evolutionary adaptation that allowed it to track spatiotemporally fluctuating resources across its landscape.

The local geography and geology place constraints on where the individual travelled during the last years of its life. The Darling Downs is bounded to the northeast, east, south and southwest by the Great Dividing Range (figure 4). The Range is as much as 900 m higher than the western fossil-bearing plains, with steep gradients and heavily wooded slopes and peaks that may have provided a geographical barrier to dispersal for large-bodied taxa such as *Diprotodon*. Indeed, *Diprotodon* remains have never been reliably recorded on the eastern side of the Range [9]. Just more than 200 km to the southwest and west, $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in bedrock are typically greater than those in the *Diprotodon* incisor, while to the far northwest they are much lower (figure 4), suggesting that the individual is unlikely to have spent significant time in those areas. Proximal to the Darling Downs fossil deposits, average $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of local, mainly basaltic and rhyolitic, bedrocks on the southern margin are 0.70567, while to the northwest, they are 0.70797 (figure 4). Those values are only slightly lower and higher, respectively, than measured values within the incisor. Thus, the individual's annual migration was most likely restricted to the Darling Downs, where it travelled northwest and

southeast across the plains, as much as 200 km per year. This hypothetical route closely tracks the upper headwaters of the Condamine River, and the individual may have used this drainage system as a migratory corridor.

Diprotodon currently appears to be unique amongst all other marsupials, and metatherians more broadly, living or extinct, in that it was a seasonal migrant. Some extant marsupials, such as red kangaroos (*Macropus rufus*), can undertake nomadic migrations [31], but no other known marsupial has been observed or inferred to make annual, repetitive, two-way trips. Independent taphonomic and palaeobiological information suggests that *Diprotodon* was gregarious [9], thus, it is most likely that the individual examined in this study undertook its migration, not alone, but rather, in a small herd or 'mob'.

Our inference of seasonal, latitudinal migration of megafauna in eastern Sahul during the Middle Pleistocene is strikingly similar to that of modern east African large mammal migrations. Thus, these findings beg the question: how common was seasonal migration in other Sahulian megafauna? At least six or seven large-bodied wombat-like diprotodontoid marsupials occurred during the Pleistocene, alongside a diverse range of other giant terrestrial kangaroos and wombats, but their role as potentially migrating herbivores remains unknown.

While Middle Pleistocene Sahul was relatively warm and wet, the period that coincided with the extinction of *Diprotodon* in the Late Pleistocene was characterized by enhanced seasonality, widespread aridity and habitat change [32]. Such changes could have overcome the ability of migratory species to adapt, and especially those that appear to have had highly specialized dietary preferences such as *D. optatum*.

Regardless, removal of wide-ranging migratory keystone megaherbivores, such as *Diprotodon*, is likely to have had significant follow-on ecological effects that could have detrimentally impacted contemporary faunas leading to extensive ecosystem reorganization over extensive geographical areas.

Data accessibility. All geochronological and geochemical data are uploaded as the electronic supplementary material.

Authors' contributions. G.J.P. conceived the study, and G.J.P., Y.J.F., G.E.W. and J.L. designed the experiments. K.J.F. conducted physical analyses of the fossil, and K.J.F., P.H., A.D.N. and R.J.-B. performed

geochemical analyses and contributed to theoretical interpretations. G.J.P., K.J.F., G.E.W., Y.-x.F., J.-x.Z. and J.L. performed computational analyses. G.J.P., G.E.W. and J.L. wrote the manuscript, with extensive input from all authors.

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