

LETTERS

An arid-adapted middle Pleistocene vertebrate fauna from south-central Australia

Gavin J. Prideaux¹, John A. Long^{1,2}, Linda K. Ayliffe^{3,4}, John C. Hellstrom⁵, Brad Pillans⁴, Walter E. Boles⁶, Mark N. Hutchinson⁷, Richard G. Roberts⁸, Matthew L. Cupper⁵, Lee J. Arnold⁸, Paul D. Devine⁹ & Natalie M. Warburton¹

How well the ecology, zoogeography and evolution of modern biotas is understood depends substantially on knowledge of the Pleistocene^{1,2}. Australia has one of the most distinctive, but least understood, Pleistocene faunas. Records from the western half of the continent are especially rare³. Here we report on a diverse and exceptionally well preserved middle Pleistocene vertebrate assemblage from caves beneath the arid, treeless Nullarbor plain of south-central Australia. Many taxa are represented by whole skeletons, which together serve as a template for identifying fragmentary, hitherto indeterminate, remains collected previously from Pleistocene sites across southern Australia. A remarkable eight of the 23 Nullarbor kangaroos are new, including two tree-kangaroos. The diverse herbivore assemblage implies substantially greater floristic diversity than that of the modern shrub steppe, but all other faunal and stable-isotope data indicate that the climate was very similar to today. Because the 21 Nullarbor species that did not survive the Pleistocene were well adapted to dry conditions, climate change (specifically, increased aridity) is unlikely to have been significant in their extinction.

The Nullarbor plain is a vast treeless expanse of chenopod shrub steppe⁴ at the centre of the 240,000 km² onshore portion of the Eucla basin⁵ (Fig. 1). In 2002, a speleological team discovered vertebrate fossils in three Nullarbor caves. Here named the Thylacoleo caves, these large collapse chambers preserve the most diverse Pleistocene fauna yet recovered from the western half of Australia. No vertebrate remains older than late Pleistocene⁶ have previously been detailed from south-central Australia. Their discovery provides a long-awaited historical perspective on the region that today acts as a barrier to the east–west dispersal of many taxa^{7,8}. Fossil preservation in the Thylacoleo caves is without precedent in Australia. Several new and previously incompletely known species are represented by whole skeletons (Fig. 2).

U/Pb ages of 4.1–3.8 Myr ago⁹ on *in situ* stalagmites in Leana's Breath cave (LBC) indicate that this cave formed before the mid-Pliocene. LBC and Flightstar cave (FSC) are each entered through a solution pipe in the chamber roof, with pitches of about 20 m to the floors below. The preservation and distribution of cave-surface fossils (decreasing concentration away from entrances) suggests that Pleistocene animals fell or flew down these same pipes before their blocking. An obstructed pipe 8 m away from the present collapse entrance of Last Tree cave (LTC) was the likely Pleistocene opening. Although most animals were evidently pitfall victims, sediments in FSC and LBC preserve a high proportion of small bones that may

derive from regurgitated pellets of roosting owls (*Tyto* species) or kestrels (*Falco cenchroides*), which are present in the fauna. Fossils occur within sediment formed from limestone breakdown, atop or wedged between boulders, and atop or buried in silty clay infill sediments (see Supplementary Information).

Three dating techniques and reconstruction of deposition processes permit the recognition of at least two intervals of faunal

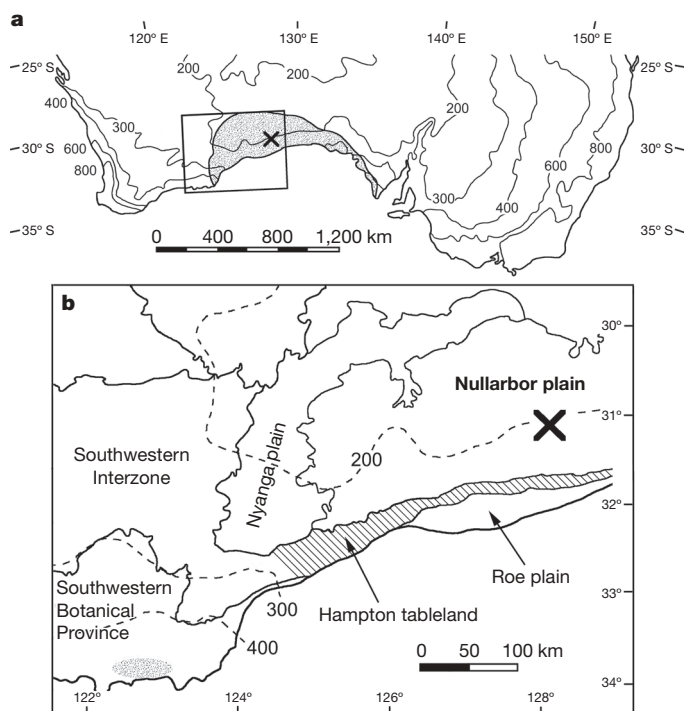


Figure 1 | Location of the Nullarbor plain and Thylacoleo caves. **a**, Southern mainland Australia, showing the Eucla basin (stippled) and mean annual rainfall isohyets (mm). **b**, Botanical regions of the western Eucla basin and surrounds^{4,5}. Nullarbor plain, unwooded shrub steppe; Hampton tableland and Roe/Nyanga plains, wooded shrub steppe and shrubland; Southwestern Botanical Province and Southwestern Interzone, shrubland, heath and mixed woodland. Dashed lines denote rainfall¹⁹. The stippled area marks the nearest modern occurrences of *Macropus eugenii* and *Egernia kingii*. The hatched area is Hampton tableland, and the cross represents the location of the Thylacoleo caves.

¹Department of Earth and Planetary Sciences, Western Australian Museum, Perth, Western Australia 6000, Australia. ²Museum Victoria, PO Box 666, Melbourne, Victoria 3001, Australia. ³Department of Geology and Geophysics, University of Utah, Salt Lake City, Utah 84112, USA. ⁴Research School of Earth Sciences, Australian National University, Canberra, Australian Capital Territory 0200, Australia. ⁵School of Earth Sciences, University of Melbourne, Melbourne, Victoria 3010, Australia. ⁶Terrestrial Zoology, Australian Museum, Sydney, New South Wales 2010, Australia. ⁷Herpetology Section, South Australian Museum, Adelaide, South Australia 5000, Australia. ⁸GeoQuEST Research Centre, School of Earth and Environmental Sciences, University of Wollongong, Wollongong, New South Wales 2522, Australia. ⁹Speleological Research Group Western Australia, PO Box 1611, East Victoria Park, Western Australia 6981, Australia.

accumulation in LBC. Palaeomagnetic samples from the infill sediment reveal a magnetic reversal between 0.5 and 0.7 m depth (see Supplementary Information). The lower sediments accumulated during the Matuyama Reversed Chron (more than 780 kyr ago). Deposition ceased when the entrance pipe became blocked. The upper sediments accumulated, after reopening of the pipe, during the Brunhes Normal Chron (less than 780 kyr ago). Optical dating of quartz grains provides a minimum age of 195 ± 15 kyr (mean \pm s.e.m.) for entry of the latter sediments into LBC. The flood responsible for a surface palaeochannel (containing partial skeletons and crania) may have induced blockage of the pipe, until its recent reopening.

In places, the upper LBC sediment overlies coralline calcite speleothems. $^{234}\text{U}/^{230}\text{Th}$ ages of 407 ± 17 , 394 ± 15 and 392 ± 24 kyr have been obtained from coralline samples, the latter encrusting a cave-surface fossil. These constrain the age of the upper sediment and its fossils to some time between 400 and 200 kyr ago (see Supplementary Information). Marked similarity in preservation suggests that most if not all of the cave-surface material exceeds 400 kyr in age. Optical dating of surface sediments in FSC and LTC provides minimum ages for fossils of 230 ± 27 kyr and 101 ± 17 kyr, respectively.

Sixty-nine vertebrate and one gastropod species have been identified in the Thylacoleo caves (see Supplementary Information). This includes 23 kangaroo species, eight of which are undescribed

(Table 1). Several are represented by complete crania and/or skeletons, facilitating the identification of three of these 'new' species among fragmentary, indeterminate material collected previously from Pleistocene sites in semi-arid southern Australia (Table 1). Herbivore diversity is similar to that of other Pleistocene assemblages^{10–12}, but the fauna from the Thylacoleo caves has proportionally fewer arboreal folivores and fungivores, and a larger number of mixed feeders and grazers, similar to the Pleistocene fauna of inland Australia (see Supplementary Information). This suggests a dry, relatively open environment.

Among the 20 mammals in the fauna that survived the Pleistocene, only *Macropus eugenii* and *Dasyercus* sp. cf. *blythi* have no regional late Holocene records^{13,14} (Fig. 1b). With the exception of a specimen tentatively identified as *Egernia kingii* (a species now restricted to the Southwestern Botanical Province), the remaining lizards are common locally or in peripheral open woodland or shrubland habitats (<http://www.amonline.net.au/herpetology/research/index.htm>) (Fig. 1b). Overall, the presence of the lizards indicates dry conditions, but with a more diverse vegetation than now exists on the Nullarbor plain. The presence of birds rules out closed woodland, but they are otherwise generalized in their habitat preferences (see Supplementary Information). However, the presence of two parrots suggests the presence of hollow-forming trees useful for nesting. The gastropod, *Pupoides adelaidae*, ranges widely today through semi-arid and arid southern Australia, including the Nullarbor plain¹⁵.

Stable carbon-isotope and oxygen-isotope ratios in herbivore teeth reflect the isotope contents of diet vegetation and ingested waters^{16,17}, which are in turn influenced by climate¹⁸. We analysed 59 enamel samples from 13 kangaroo and 1 wombat species in the Thylacoleo caves fauna, and compared these with a data set based on modern grazing kangaroo and wombat specimens (Fig. 3) from the winter, uniform and arid/non-seasonal rainfall zones of southern Australia^{3,19}. Low summer rainfall in southern Australia determines the predominance of C_3 grasses in areas of low, medium and high rainfall (Fig. 3a). In the Nullarbor region, modern samples from the Hampton tableland (Fig. 1b) lie within the C_3 range, whereas those from the northern Nullarbor plain give mixed (C_3 and C_4) signatures (Fig. 3b). $\delta^{13}\text{C}$ values for Pleistocene herbivores from the Thylacoleo

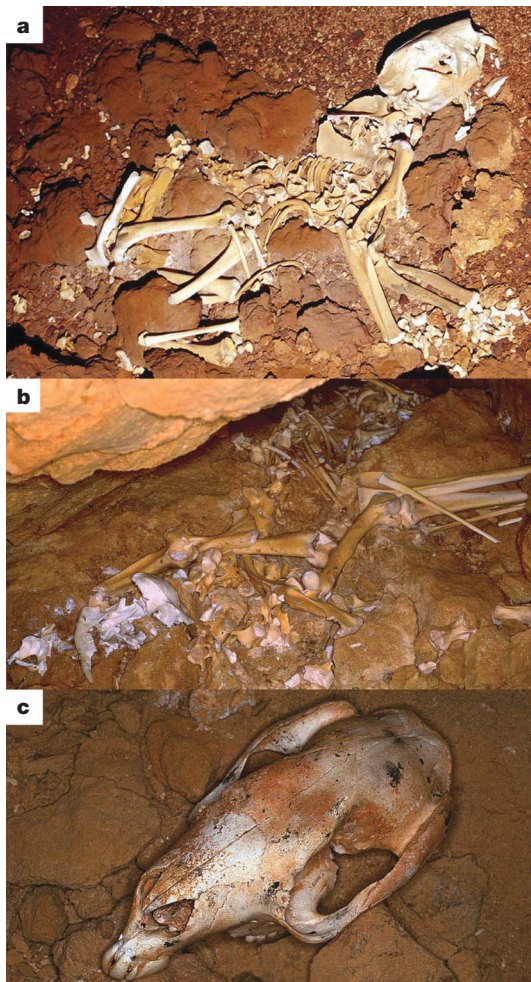


Figure 2 | Fossils from the Thylacoleo caves. a, Complete skeleton of *Thylacoleo carnifex* (WAM 02.7.1). **b**, Complete skeleton of *Baringa* sp. nov. 1 (WAM 02.7.17). This unusual kangaroo is the most common marsupial in the fauna, and bore high-crowned incisors and enlarged tuberosities above its eye orbits. **c**, Cranium of *Sthenurus andersoni* (WAM 03.5.5).

Table 1 | Species in the Thylacoleo caves fauna that did not survive the Pleistocene

Species	Rainfall range (mm)		Body mass (kg)
	Lower	Upper	
<i>Leipoa gallinacea</i> *	200	690	10
<i>Phascolonus gigas</i> *	150	800	200
<i>Thylacoleo carnifex</i> *	150	1,200	80
<i>Baringa</i> sp. nov. 1	–	260	30
<i>Baringa</i> sp. nov. 2	–	–	20
<i>Baringa</i> sp. nov. 3	–	–	30
<i>Bohra</i> sp. nov. 1	–	500	25
<i>Bohra</i> sp. nov. 2	–	–	25
<i>Congruus kitcheneri</i> *	–	1,000	40
<i>Congruus</i> sp. nov. 1	–	250	50
<i>Congruus</i> sp. nov. 2	–	–	50
<i>Macropus ferragus</i> *	150	800	150
<i>Macropus</i> sp. nov.	150	1,000	35
<i>Metasthenurus newtonae</i> *	260	1,200	55
<i>Procoptodon goliah</i> *	100	800	200
' <i>Procoptodon</i> ' <i>browneorum</i> *	250	1,000	60
' <i>Procoptodon</i> ' <i>williamsi</i>	150	600	120
<i>Protemnodon brehus</i> *	150	1,000	100
<i>Protemnodon roechus</i> *	150	800	120
<i>Sthenurus andersoni</i> *	100	1,000	50
<i>Sthenurus tindalei</i> *	100	300	100
Minimum	100	260	10
Maximum	260	1,200	200

Estimated rainfall bounds (upper and lower) are based on the modern mean annual rainfall¹⁹ across Pleistocene ranges³. The four species with neither bound are unknown outside of the Thylacoleo caves; those lacking a lower bound are known from only one other site. Body masses are from ref. 29 or have been estimated from a comparison with closest-sized living species. Species marked by an asterisk have late Pleistocene records.

caves (-13.3 to -7.2% ; $n = 41$) cluster between the modern Hampton tableland and northern Nullarbor samples (Fig. 3b).

Modern samples from warmer, drier areas of southern Australia yield enamel $\delta^{18}\text{O}$ values that are more positive than those from cooler, wetter areas (Fig. 3a). $\delta^{18}\text{O}$ values from the Hampton tableland (mean annual rainfall 240–270 mm) herbivores range from -4.4 to 4.2% ($n = 71$), whereas those from the northern Nullarbor (180 mm) range from 2.0 to 8.4% ($n = 5$) (Fig. 3b). The Pleistocene herbivores yield $\delta^{18}\text{O}$ values (-0.1 to 7.6% ; $n = 40$) intermediate between those of the modern samples (Fig. 3b), despite slight differences between sites that may or may not (given low sample sizes) reflect slight variations in prevailing climate due to site age differences. Nevertheless, the overriding climatic implication of the isotope data is manifest: effective precipitation and seasonality during the intervals over which the Pleistocene fauna accumulated were similar to those of the present, in which an annual mean of about 200 mm falls in a largely non-seasonal, but slightly winter-biased, pattern¹⁹.

Thirty-one of the 36 Thylacoleo caves species that survived the Pleistocene have recent records in the region^{13,14}. Estimated from modern tolerances (see Supplementary Information), all species except *Macropus eugenii* and *Egernia* sp. cf. *kingii* could have coexisted within a 230–250-mm mean annual rainfall range. Factors controlling the modern distribution of *M. eugenii* and *E. kingii* are uncertain, but it is likely that shrub diversity, not rainfall, is a key determinant. Modern rainfall across the former ranges³ of the 21 species that became extinct before the Holocene (excluding the four known only from the Thylacoleo caves) suggests that they could have cohabited an area with a rainfall of about 260 mm (Table 1). Together

with the modern faunal and isotope data, these indicate a predominantly arid climate with a palaeorainfall range of 230–260 mm.

Cave sediments are too oxidized to preserve pollen, but the high diversity of herbivores reflects a profoundly different vegetation structure from that of the modern chenopod steppe. No species exemplify this more than the tree-kangaroos (*Bohra*), whose modern relatives (*Dendrolagus*) inhabit rainforest. In stark contrast, however, *Bohra* species were not restricted to well-wooded habitats³, and probably represent the hitherto ‘missing’ arboreal folivores of the semi-arid and arid woodlands of late Cenozoic Australia. The varied morphologies and broad size range (4–200 kg) of the 20 terrestrial browsing and/or grazing marsupials (Table 1; Supplementary Information) indicate a scleromorphic mosaic of woodland and shrubland incorporating a higher proportion of plants with palatable leaves and fleshy fruits (for example, species of Myoporaceae, Santalaceae, Pittosporaceae and Lorantheaceae), such as those now largely confined to remnant stands on the Nullarbor periphery^{4,20} (Fig. 1b; see Supplementary Information). Loss of a similar range of fire-sensitive plants, and their replacement by fire-adapted mulga woodland and spinifex grassland, as a result of landscape burning by humans has been advanced as a cause of the extinction in central Australia of the giant flightless bird *Genyornis*^{21,22}.

By establishing that the Nullarbor Pleistocene fauna was adapted to dry conditions, extinction hypotheses invoking megafaunal susceptibility to aridity^{23,24} become untenable. Even during the driest times, ranges of the less arid-adapted species could simply have shifted more peripherally. Indeed, 12 of the 13 described Nullarbor megafaunal species survived into the late Pleistocene elsewhere, and were common in drier areas^{3,11,25} (Table 1). It follows that climate change alone is unlikely to have precipitated the demise of this remarkable fauna, particularly in view of other evidence that Australian megafaunal species were resilient to glacial–interglacial cycling¹⁰. We argue that increased wildfires in the Nullarbor region best explain the conversion of a floristically diverse plant community into the modern, fire-resistant, chenopod shrub steppe. Although capable of supporting abundant vegetation, limestone substrates are inherently infertile, with nutrients held in thin upper soil horizons highly susceptible in arid areas to pyrogenic denudation²⁶. Our data do not directly explain the timing of extinctions, but it is significant that the general extinction pattern (the loss of most larger herbivores and *Thylacoleo*) is identical to that witnessed in all southern Australian climatic zones^{10,12,25}. Most southern species of megafauna were evidently extinct by or soon after 40 kyr ago^{6,12,25}, at about the time humans reached the south-central coast²⁷.

METHODS

Palaeontology. Fossils were photographed *in situ* and locations were recorded relative to cave survey points. All specimens were extremely fragile and required hardening with polyvinyl butyrate dissolved in 100% ethanol before being wrapped and removed from sites in hard plastic cases. On all occasions, great care was taken to preserve element associations. Sediments were removed from the LBC test excavation in 10-cm levels and wet-screened for small vertebrate remains. All specimens are lodged in the Western Australian Museum, Perth.

Geochronology. ²³⁴U/²³⁰Th dating was conducted on solid pieces of calcite weighing 3–30 mg, cut from the speleothem samples with a dental drill. Multiple subsamples were taken from each coralline crust to assess the degree of open-system behaviour for these samples. Eight oriented monoliths ($10 \times 10 \times 5 \text{ cm}^3$) were carefully excavated from a $0.5 \text{ m}^2 \times 1.3 \text{ m}$ -deep test pit in sediments in LBC to assess palaeomagnetism. Standard palaeomagnetic samples ($2 \times 2 \times 2 \text{ cm}^3$) were prepared from each monolith. Three samples from each monolith were measured on a 2G Enterprises three-axis cryogenic magnetometer. Stepwise alternating field demagnetization (peak field 140 mT) was undertaken to isolate characteristic remanent magnetizations, which were determined by principal components analysis. Optical dating provides an estimate of time elapsed since luminescent minerals, such as quartz, were last exposed to sunlight²⁸. In this study, the event being dated was the time of entry of sediment grains into the caves. Optical ages for buried quartz grains were calculated from the burial dose (estimated from the optically stimulated luminescence signal) divided by the dose rate due to ionizing radiation.

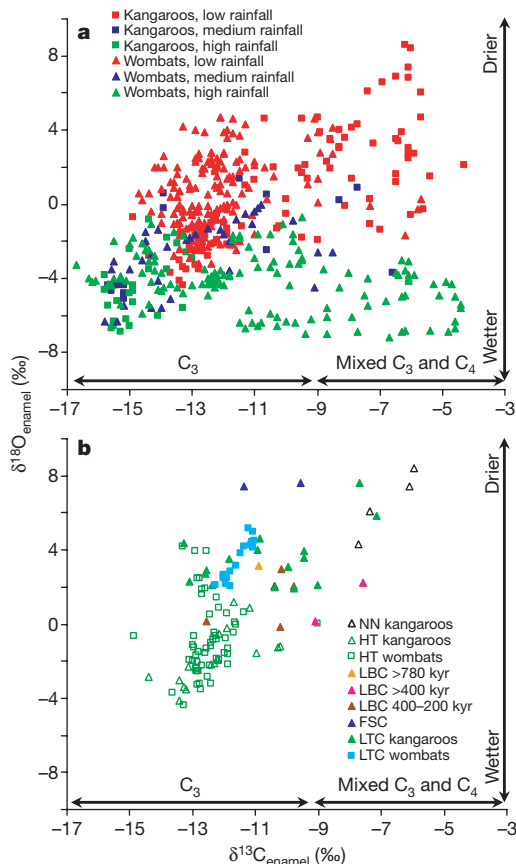


Figure 3 | Stable carbon-isotope and oxygen-isotope values ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) from the enamel of kangaroos and wombats. a, Modern samples from the winter, uniform and arid/non-seasonal rainfall zones of southern Australia^{3,19}. Low rainfall, less than 300 mm; medium rainfall, 350–550 mm; high rainfall, more than 600 mm. b, Isotope ratios of fossil samples from the Thylacoleo caves (LBC, FSC, LTC) compared with those of modern samples from the Hampton tableland (HT) and northern Nullarbor plain (NN).

Stable isotopes. Samples of powdered enamel from fourth molars were subjected to 15-min treatments with 3% hydrogen peroxide followed by 0.1 M acetic acid with several intervening rinses with demineralized water. Samples of 0.5–1.0 mg were reacted at 90 °C in a common acid bath. Evolved gases were cryogenically purified of H₂O and transferred to a microvolume cold finger before analysis through the dual inlet of a Finnigan MAT 252 mass spectrometer. Isotope results were standardized to the Pee Dee Belemnite scale by in-run comparison of enamel standards calibrated against NBS-19. $\delta^{13}\text{C}$, $\delta^{18}\text{O} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1,000$, where R is the $^{13}\text{C}/^{12}\text{C}$ or $^{18}\text{O}/^{16}\text{O}$ ratio.

Received 25 August; accepted 21 November 2006.

- FAUNMAP Working Group. Spatial response of mammals to Late Quaternary environmental fluctuations. *Science* **272**, 1601–1606 (1996).
- Lister, A. M. The impact of Quaternary Ice Ages on mammalian evolution. *Phil. Trans. R. Soc. Lond. B* **359**, 221–241 (2004).
- Prideaux, G. J. in *Encyclopedia of Quaternary Science* (ed. Elias, S.) 1518–1537 (Elsevier, Oxford, 2006).
- Beard, J. S. *Vegetation Survey of Western Australia: Nullarbor. 1:1,000,000 Vegetation Series. Explanatory Notes to Sheet 4* (University of Western Australia, Perth, 1975).
- Lowry, D. C. Geology of the Western Australian part of the Eucla Basin. *Geol. Surv. West. Aust. Bull.* **122**, 1–201 (1970).
- Lundelius, E. L. & Turnbull, W. D. The mammalian fauna of Madura Cave, Western Australia. Part VII: Macropodidae: Sthenurinae, Macropodinae, with a review of the marsupial portion of the fauna. *Fieldiana Geol.* **ns 17**, 1–71 (1989).
- Burbidge, N. T. The phytogeography of the Australian region. *Aust. J. Bot.* **8**, 75–212 (1960).
- Keast, A. (ed.) *Ecological Biogeography of Australia* (W. Junk, The Hague, 1981).
- Woodhead, J. et al. U–Pb geochronology of speleothems by MC-ICPMS. *Quat. Geochronol.* **1**, 208–221 (2006).
- Prideaux, G. J. et al. Mammalian responses to Pleistocene climate change in southeastern Australia. *Geology* **35**, 33–36 (2007).
- Prideaux, G. J. *Systematics and Evolution of the Sthenurine Kangaroos* (Univ. Calif. Publ. Geol. Sci. no. 146, 2004).
- Prideaux, G. J., Gully, G. A., Ayliffe, L. K., Bird, M. I. & Roberts, R. G. Tight Entrance Cave, southwestern Australia: a late Pleistocene vertebrate deposit spanning more than 180 ka. *J. Vertebr. Paleontol.* **20**, 62A–63A (2000).
- Baynes, A. in *A Biological Survey of the Nullarbor Region, South and Western Australia in 1984* (eds McKenzie, N. L. & Robinson, A. C.) 139–152 (Department of Environment and Planning, Adelaide, 1987).
- Strahan, R. (ed.) *The Mammals of Australia* (Reed New Holland, Sydney, 1995).
- Solem, A. Pupilloid land snails from the south and mid-west coasts of Australia. *J. Malacol. Soc. Aust.* **7**, 95–124 (1986).
- Passey, B. H. et al. Carbon isotope fractionation between diet, breath CO₂, and bioapatite in different mammals. *J. Archaeol. Sci.* **32**, 1459–1470 (2005).
- Cerling, T. E. et al. The reaction progress variable in stable isotope studies of biological tissue turnover. *Oecologia* (in the press).
- Koch, P. L. Isotopic reconstruction of past continental environments. *Annu. Rev. Earth Planet. Sci.* **26**, 573–613 (1998).
- Bureau of Meteorology. *Climate of Australia* (Australian Government Publishing Service, Canberra, 1989).
- Mitchell, A. A. & Wilcox, D. G. *Arid Shrubland Plants of Western Australia* (Univ. of Western Australia Press, Perth, 1998).
- Miller, G. H. et al. Ecosystem collapse in Pleistocene Australia and a human role in megafaunal extinction. *Science* **309**, 287–290 (2005).
- Murray, P. F. & Vickers-Rich, P. *Magnificent Mihirungs: The Colossal Flightless Birds of the Australian Dreamtime* (Univ. of Indiana Press, Bloomington, Indiana, 2004).
- Horton, D. R. in *Quaternary Extinctions: A Prehistoric Revolution* (eds Martin, P. S. & Klein, R. G.) 639–680 (Univ. of Arizona, Tucson, 1984).
- Wroe, S. & Field, J. A review of the evidence for a human role in the extinction of Australian megafauna and an alternative interpretation. *Quat. Sci. Rev.* **25**, 2692–2703 (2006).
- Roberts, R. G. et al. New ages for the last Australian megafauna: continent-wide extinction about 46,000 years ago. *Science* **292**, 1888–1892 (2001).
- McKenzie, N. J., Jacquier, D., Isbell, R. F. & Brown, K. *Australian Soils and Landscapes: An Illustrated Compendium* (CSIRO Publishing, Melbourne, 2004).
- Roberts, R. G. et al. Preliminary luminescence dates for archaeological sediments on the Nullarbor Plain, South Australia. *Aust. Archaeol.* **42**, 7–16 (1996).
- Lian, O. B. & Roberts, R. G. Dating the Quaternary: progress in luminescence dating of sediments. *Quat. Sci. Rev.* **25**, 2449–2468 (2006).
- Johnson, C. N. & Prideaux, G. J. Extinctions of herbivorous mammals in Australia's late Pleistocene in relation to their feeding ecology: no evidence for environmental change as cause of extinction. *Aust. Ecol.* **29**, 553–557 (2004).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements We thank P. Ackroyd, K. Boland, R. Gibbons, G. MacLucas, J. MacLucas and E. Taylor for bringing their discoveries to our attention, and for cave mapping and field assistance; C. Bryce, G. Deacon, L. Hatcher, D. Megirian and M. Norton for field assistance; G. Kendrick and A. Baynes for identifying gastropod and rodent fossils, respectively; and P. Latz, J. Magee, D. Megirian, G. Miller and P. Murray for discussions. This study was supported by two grants from the Rio Tinto WA Future Fund to the Western Australian Museum. Isotopic analysis was funded by a US National Science Foundation grant.

Author Contributions G.J.P. was responsible for site descriptions, faunal analysis, data synthesis and writing the paper, J.A.L. fieldwork coordination, L.K.A. stable isotope analysis, J.C.H. U-series dating, B.P. magnetic polarity assessment, M.N.H. lizard identifications, W.E.B. bird identifications, R.G.R., M.L.C. and L.J.A. optical dating, P.D.D. site interpretation, and N.M.W. small marsupial identifications.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Correspondence and requests for materials should be addressed to G.J.P. (gavin.prideaux@museum.wa.gov.au).