CORRECTED 17 MARCH 2025; SEE LAST PAGE

EVOLUTION

Dietary breadth in kangaroos facilitated resilience to Quaternary climatic variations

Samuel D. Arman[1,2]*, Grant A. Gully[2], Gavin J. Prideaux[2]

Identifying what drove the late Pleistocene megafaunal extinctions on the continents remains one of the most contested topics in historical science. This is especially so in Australia, which lost 90% of its large species by 40,000 years ago, more than half of them kangaroos. Determining causation has been obstructed by a poor understanding of their ecology. Using dental microwear texture analysis, we show that most members of Australia's richest Pleistocene kangaroo assemblage had diets that were much more generalized than their craniodental anatomy implies. Mixed feeding across most kangaroos pinpoints dietary breadth as a key behavioral adaptation to climate-driven fluctuations in vegetation structure, dispelling the likelihood that late Pleistocene climatic variation was a primary driver of their disappearance.

Intrinsic traits that may make a species vulnerable to extinction include small geographic range, rarity, large body size, and high specialization (*1*). However, there has been little explicit exploration of the influence of such factors on late Pleistocene extinction patterns, with the exception of body size (*2*). Rather, support for one causal hypothesis over another has primarily been drawn from how well putative environmental stressors and species extinctions align in time and space. In Australia, extinctions were concentrated within the interval of 65,000 to 40,000 years ago, which corresponds with the first 25,000 years of human presence on the landscape, leading to debate over the primacy of human impacts and coincident climatic changes (*3*–*7*).

Among the groups affected by extinction, kangaroos had been by far the most speciose, having radiated in response to increasing aridity through the late Cenozoic, reaching peak diversity in the last one million years (*8*, *9*). This underscores the peculiarity of their decline in the late Pleistocene, when most large-bodied forms became extinct, including at least 12 sthenurines ("short-faced" kangaroos) and at least 11 macropodines (*3*, *4*, *7*, *8*, *10*–*12*). To assess whether dietary specialization may have made some kangaroos more vulnerable to environmental change (*5*, *7*), it is essential to resolve what these species ate.

Most modern macropodines are grazers (consumers of grass and forbs) or mixed feeders (consumers of both dicots and grass) (*13*). By contrast, the craniodental morphology of sthenurines suggests that they were adapted for consuming tough dicot browse (*8*, *10*, *14*). However, until now there has been sparse direct evidence for their diets (*6*, *15*). We present the largest-ever dental microwear texture analysis (DMTA) dataset, composed of 2650 scans taken from 937 individual specimens to characterize diets of kangaroo species found within

[1]Museum and Art Gallery of the Northern Territory, Alice Springs, Northern Territory, Australia. [2]College of Science and Engineering, Flinders University, Bedford Park, South Australia, Australia.
*Corresponding author. Email: samuel.arman@magnt.net.au

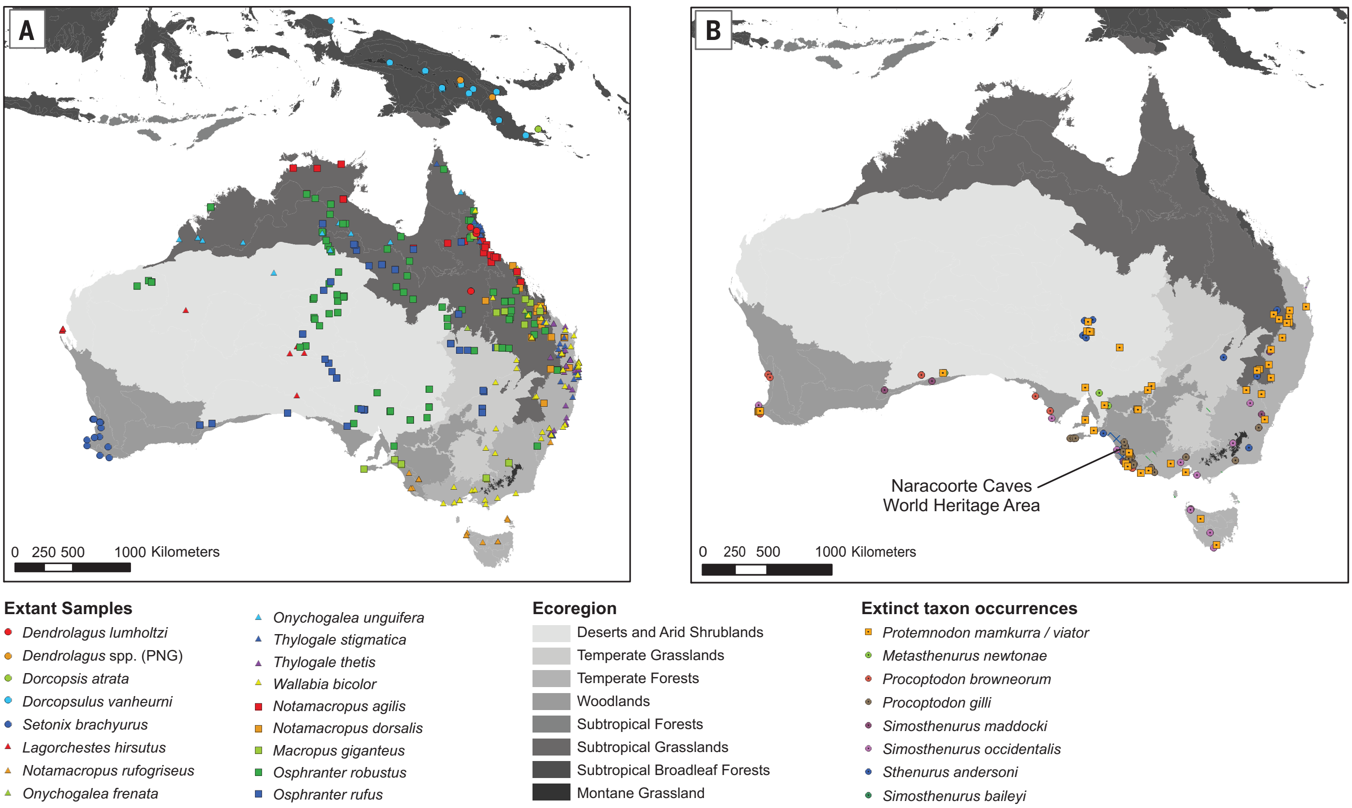

Fig. 1. Geographic data for kangaroo species used in this study. (**A**) Sample locations for modern specimens. Circles, browsers; triangles, mixed feeders; squares, grazers. (**B**) Recorded occurrences of extinct species and ranges of extant species sampled here from Victoria Fossil Cave, Naracoorte Caves World Heritage Area (*10*, *39*). Circles, Sthenurinae; squares, the extinct macropodine *Protemnodon mamkurra / viator* (*12*). Ecoregions in (A) and (B) are from (*40*).

Table 1. Microwear dietary consensus. Consensus diet as inferred from DMTA data and analyses. Described diet for extant species from (*13*) and for extinct taxa see table. Confidence here reflects an informal inference in which low sample sizes or conflicting results for some variables limits the scope of dietary inference.

Group	Species	Described diet	Microwear diet	Confidence
Modern browsers	*Dendrolagus lumholtzi*	Browse	Unclear	-
	Dendrolagus spp. (PNG)	Browse	Unclear	-
	Dorcopsis atrata	Browse	Unclear	-
	Dorcopsulus vanheurni	Browse	Unclear	-
	Setonix brachyurus	Browse	Browse	High
Modern mixed feeders	*Notamacropus rufogriseus*	Mixed–browse	Mixed	High
	Onychogalea frenata	Mixed	Mixed	Low
	Onychogalea unguifera	Mixed	Mixed	Low
	Thylogale stigmatica	Mixed	Mixed–grass	Mid
	Thylogale thetis	Mixed	Mixed–browse	Low
	Wallabia bicolor	Mixed	Mixed (generalist)	High
Modern grazers	*Lagorchestes hirsutus*	Seed specialist	Browse	Mid
	Notamacropus agilis	Grass	Grass	Mid
	Notamacropus dorsalis	Grass	Grass (obligate)	High
	Macropus giganteus	Grass	Grass (facultative)	High
	Osphranter robustus	Grass	Grass (facultative)	High
	Osphranter rufus	Grass	Grass (obligate)	High
VFC macropodines	*Macropus giganteus* (VFC)	Graze	Mixed–browse	High
	Notamacropus greyi	Mixed (*41*)	Mixed–browse	Mid
	Notamacropus rufogriseus (VFC)	Mixed–browse	Mixed–browse	High
	Protemnodon mamkurra	Various (*6*, *10*, *24*, *25*)	Grass (obligate)	Mid
	Wallabia bicolor (VFC)	Mixed	Browse	High
VFC sthenurines	*Metasthenurus newtonae*	Browser (*10*)	Mixed–browse	High
	Procoptodon browneorum	Browser (*10*)	Mixed–browse	High
	Procoptodon gilli	Browser (*10*)	Mixed–browse	High
	Simosthenurus baileyi	Browser (*10*)	Browse	Low
	Simosthenurus maddocki	Browser (specialist) (*10*)	Browse (obligate)	High
	Simosthenurus occidentalis	Browser (specialist) (*10*, *14*)	Browse (obligate)	High
	Sthenurus andersoni	Mixed (*42*)	Mixed	Mid

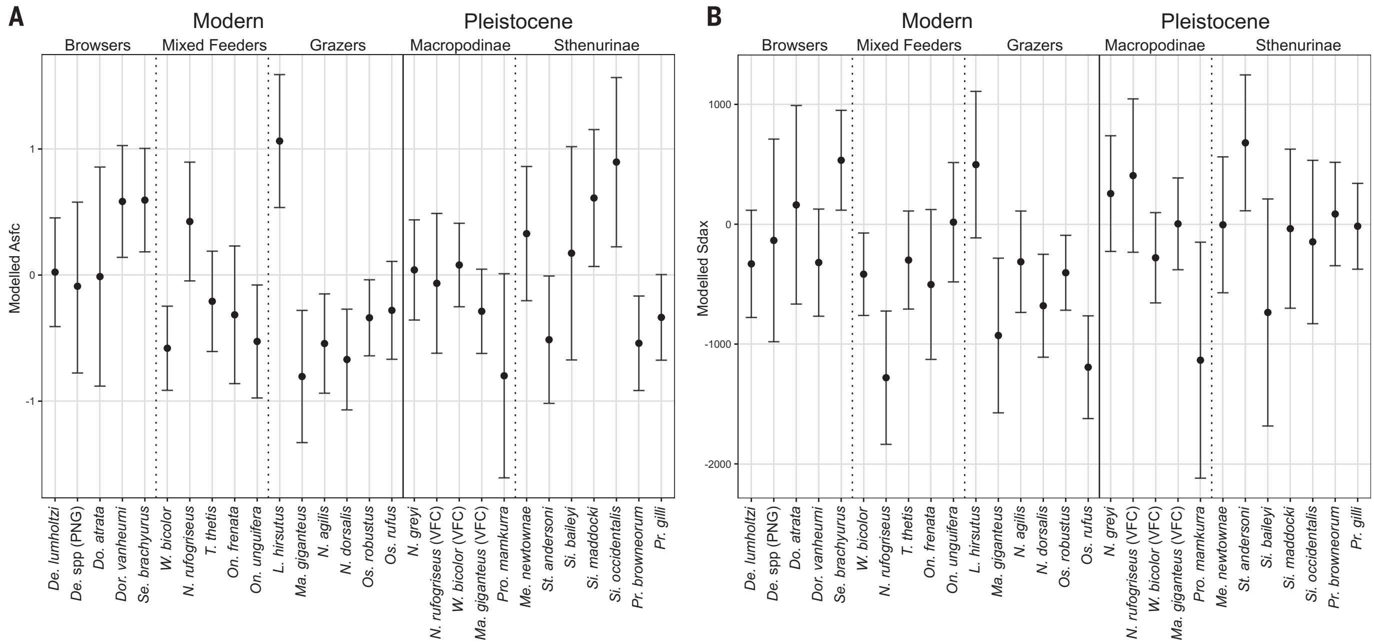

Fig. 2. Mean modeled microwear for selected modeled DMTA variables. (**A**) Linear mixed-effect models of microwear between species for area-scale fractal complexity (Asfc) (**B**) maximum width of hills (Sdax). Variables were chosen as those which best exemplify dietary differences broadly across the dataset. For descriptions of DMTA variables and models used, see table S5; for all variables, see figs. S4 to S6.

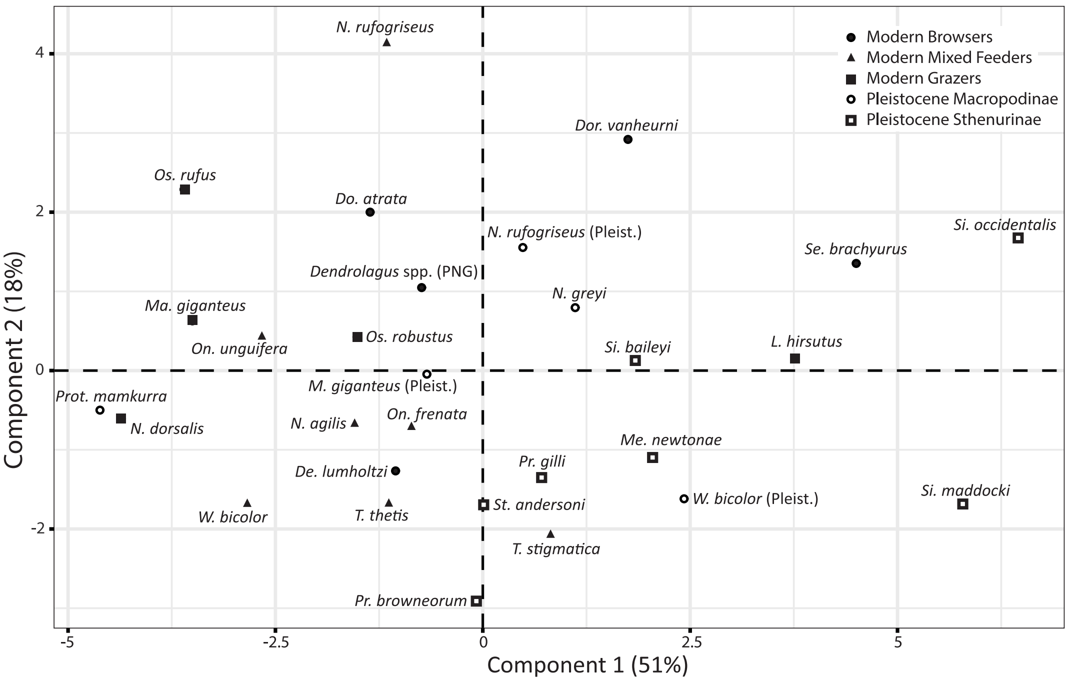

Fig. 3. Principal components 1 and 2 of mean DMTA data for all taxa. Component 1 is considered indicative of the dietary spectrum, with grazers left and browsers right. Details and interpretation of the PCA can be found in the materials and methods and figure S7.

Australia's most diverse Pleistocene kangaroo fossil assemblage. Wear caused by chewing foods with different material properties leaves distinctive microscopic texture patterns on tooth enamel, and DMTA uses scale-sensitive fractal geometry and International Organization for Standardization parameters to quantify these wear patterns (*16–18*).

Microwear signatures of the 12 best-represented kangaroo species, including extinct and extant taxa, from the Main Fossil Chamber deposit of Victoria Fossil Cave (VFC), Naracoorte Caves World Heritage Area, in southeastern Australia (*10, 19*) (Fig. 1 and table S1) were compared statistically with those of 16 modern kangaroo species across the dietary spectrum (Tables 1 and S1). The VFC deposit ceased accumulating around 220,000 years ago and spans at least one glacial–interglacial cycle (*20–22*). Climatic and pollen records from the Naracoorte Caves show that, within cycles, local conditions fluctuated between cool, moist glacial and warm, dry interglacial intervals (*23*).

Linear mixed-effect modeling of DMTA data reveal dietary differences between species statistically verified by analysis of variance comparisons and visualized through principle component analysis (PCA) of mean data (Figs. 2 and 3 and S4 to S7; materials and methods). Modern DMTA exemplars include the browser *Setonix brachyurus*; mixed feeders *Wallabia bicolor* and *Notamacropus rufogriseus*; facultative grazers *Macropus giganteus* and *Osphranter robustus*; and obligate grazers *Osphranter rufus* and *Notamacropus dorsalis* (Table 1 and supplementary text). VFC species exhibit microwear signatures that largely fall within this modern dietary spectrum, with both macropodine and sthenurine taxa clearly displaying high levels of mixed feeding alongside browsing in the Pleistocene.

The four most abundant and best-sampled species—the macropodines *N. rufogriseus* and *M. giganteus* and sthenurines *Procoptodon browneorum* and *P. gilli*—show marked and distinct relative-abundance trajectories through time, indicating species-specific responses to environmental fluctuations. However, no statistically significant differences in microwear are evident through time for any of these four species (supplementary text and figs. S11 to S13). Dietary change is manifested at the subfamily level (although nonsignificant), with sthenurines and macropodines paralleling each other (figs. S11 to S13). This suggests that the dietary breadth exhibited by these morphologically different groups provided adequate flexibility to respond to any climate-driven shifts in vegetation.

The strongest grazing signature across the entire dataset characterized the extinct macropodine *Protemnodon mamkurra,* which has previously been interpreted as a browser, mixed feeder, or grazer based on different dietary proxies (*6, 10, 24, 25*). All other VFC macropodines had microwear consistent with mixed feeding and browsing. VFC sthenurines exhibit diets from mixed feeding (e.g., *Sthenurus andersoni*) to obligate browsing (e.g., *Simosthenurus maddocki*), with the differences between sthenurine species indicative of niche partitioning (Figs. 2 and 3 and Table 1).

In contrast to the long-established view of large kangaroos as dietary specialists (*6, 10, 11, 26*), DMTA suggests that mixed feeding was common in the VFC assemblage. This strategy has generally been deemed of marginal evolutionary and ecological importance and typical of only a few small-bodied Pleistocene and modern taxa (*11, 27*). Evidence of mixed feeding has lain hidden in plain view because researchers have largely judged diet from morphology: sthenurines were inferred to be built for processing tough browse vegetation whereas macropodines were inferred to be built for eating grass (*8, 10, 13*). Such adaptations likely allowed sthenurine species to fall back to consuming tougher resources when more preferable forage was scarce, but for the most part their diets were mixed. In fact, mixed feeding is more common among modern kangaroos than has often been recognized (*13, 14*) and was an attribute of Pliocene species (*9, 24*). Disparities between microwear signatures and morphology-based dietary inferences have been observed in hominins (*28*), ruminants (*29*), and now marsupials. This emphasizes the need to effectively evaluate the diets of a broader array of large Pleistocene mammals to test prevailing views of dietary specialization and extinction susceptibility in different groups, regions, and continents.

A minimum of 27 species of kangaroo became extinct in the late Pleistocene (table S6). Their loss, alongside many other large species, would have influenced the functioning of Australian ecosystems in ways that we are only beginning to conceptualize (*26*, *30*, *31*). Arguments ascribing these extinctions to "climatic deterioration" have claimed that either increased aridity drove the rise of grasslands and decline of dicots upon which "specialist" browsers were dependent (*6*, *11*, *32*), or that the reduction of grasslands favored wooded habitats and negatively affected grazers (*7*). Moreover, it is now evident that Southern Hemisphere glacial cycles were more benign and nuanced than previously asserted (*23*). The covert inference is that most large species were maladapted to environmental changes of the direction and magnitude witnessed 65,000 to 40,000 years ago, and so became extinct across the continent, through all ecoregions. Yet, extinct species that we demonstrate to have occupied different positions across the entire dietary spectrum were among the last-surviving species, persisting in different corners of the continent until c. 40,000 years ago (Fig. 1 and tables S4 and S7) (*33*).

Rather than specialists bound to a single resource, our evidence points to an inherent capacity of most kangaroos to exploit a range of foods, with diets influenced at least as much by the availability of different foods as they are by craniodental form. The three extinct species that expressed any degree of specialization occupied opposing ends of the dietary spectrum: *Prot. mamkurra* was a specialist grazer whereas *Si. maddocki* and *Si. occidentalis* were specialist browsers. They cannot have been simultaneously driven to extinction by the loss of a particular dietary resource, one favored in drier times and one in moister times. Having persisted through a succession of glacial–interglacial cycles in the Naracoorte region (*23*, *34*), nothing about the diets of large kangaroos can be taken to imply vulnerability to climatic change during the last glacial. This is consistent with the offshore record of vegetation change from southeastern Australia, which has been argued to have been a consequence, rather than a cause, of large herbivore extinctions (*30*, *35*). Although extinction scenarios invoking rapid, continent-wide extinctions (*3*) are now seen as oversimplified (*4*, *7*, *32*), the strong body size selectivity is most consistent with human predation pressure (*2*, *36*, *37*).

REFERENCES AND NOTES

1. M. L. McKinney, *Annu. Rev. Ecol. Syst.* **28**, 495–516 (1997).
2. F. A. Smith, R. E. Elliott Smith, S. K. Lyons, J. L. Payne, *Science* **360**, 310–313 (2018)
3. R. G. Roberts *et al*., *Science* **292**, 1888–1892 (2001).
4. G. J. Prideaux *et al*., *Proc. Natl. Acad. Sci. U.S.A.* **107**, 22157–22162 (2010).
5. F. Saltré *et al*., *Nat. Commun.* **7**, 10511 (2016).
6. L. R. G. DeSantis, J. H. Field, S. Wroe, J. R. Dodson, *Paleobiology* **43**, 181–195 (2017).
7. S. A. Hocknull *et al*., *Nat. Commun.* **11**, 2250 (2020).
8. G. J. Prideaux, N. M. Warburton, *Zool. J. Linn. Soc.* **159**, 954–987 (2010).
9. A. M. C. Couzens, G. J. Prideaux, *Science* (1979) 362, 72–75 (2018).
10. G. J. Prideaux, *Univ. Calif. Publ. Geol. Sci.*, **146**, pp. 1–623 (2004).
11. L. Dawson, *Alcheringa* **30**, 89–114 (2010).
12. I. A. R. Kerr, A. B. Camens, J. D. van Zoelon, T. H. Worthy, G. J. Prideaux, *Megataxa* **11**, 1–261 (2024).
13. S. D. Arman, G. J. Prideaux, *Austral Ecol.* **40**, 909–922 (2015).
14. D. R. Mitchell, *PLOS ONE* **14**, e0221287 (2019).
15. G. J. Prideaux *et al*., *Proc. Natl. Acad. Sci. U.S.A.* **106**, 11646–11650 (2009).
16. P. S. Ungar, C. A. Brown, T. S. Bergstrom, A. Walkers, *Scanning* **25**, 185–193 (2006).
17. I. Calandra, G. Merceron, *Mammal Rev.* **46**, 215–228 (2016).
18. P. S. Ungar, *BEER'N'BONES* **6**, 9–13 (2011).
19. R. T. Wells, K. Moriarty, D. L. G. Williams, *Aust. Zool.* **21**, 305–333 (1984).
20. L. K. Ayliffe *et al*., *Geology* **26**, 147–150 (1998).
21. L. J. Arnold *et al*., *Quat. Geochronol.* **70**, 101301 (2022).
22. R. Grün, K. Moriarty, R. Wells, *J. Quaternary Sci.* **16**, 49–59 (2001).
23. R. Weij *et al*., *Nature* **626**, 319–326 (2024).
24. S. Montanari, J. Louys, G. J. Price, *PLOS ONE* **8**, e66221 (2013).
25. K. Butler, J. Louys, K. Travouillon, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **408**, 11–25 (2014).
26. C. N. Johnson, *Proc. Biol. Sci.* **276**, 2509–2519 (2009).
27. G. D. Sanson, in *Kangaroos, Wallabies and Rat-Kangaroos*, G. Grigg, P. J. Jarman, I. D. Hume, Eds. (Surrey Beatty & Sons, 1989), pp. 151–168.
28. R. S. Scott *et al*., *Nature* **436**, 693–695 (2005).
29. J. P. Gailer, I. Calandra, E. Schulz-Kornas, T. M. Kaiser, *J. Mamm. Evol.* **23**, 369–383 (2016).
30. R. A. L. dos Santos *et al*., *Nat. Geosci.* **6**, 627–631 (2013).
31. G. D. Cook, W. J. Bond, E. C. February, R. J. Williams, in *Savanna woody plants and large herbivores*, P. F. Scogings, M. Sankaran, Eds. (Wiley, 2019), pp. 51–75.
32. S. Wroe, J. Field, *Quat. Sci. Rev.* **25**, 2692–2703 (2006).
33. R. Gillespie *et al*., *Quat. Sci. Rev.* **37**, 38–47 (2012).
34. G. J. Prideaux *et al*., *Geology* **35**, 33–36 (2007).
35. M. A. Adeleye *et al*., *Quat. Sci. Rev.* **316**, 108263 (2023).
36. F. A. Smith *et al*., *Cambridge Prisms: Extinction* **1**, e9 (2023).
37. M. M. Pires, *Annu. Rev. Earth Planet. Sci.* **52**, 133–158 (2024).
38. S. D. Arman, G. A. Gully, G. J. Prideaux, Macropodid Microwear associated with Dietary breadth in kangaroos facilitated resilience to Quaternary climatic variations, Dryad (2024); https://doi.org/10.5061/dryad.4j0zpc8nf.
39. G. J. Prideaux, *Mid-Pleistocene Vertebrate Records* (Elsevier, 2006).
40. D. M. Olson *et al*., *Bioscience* **51**, 933–938 (2001).
41. S. Van Dyck, R. Strahan, *The Mammals of Australia* (New Holland Publishers, 2008).
42. R. T. Wells, R. H. Tedford, *Bulletin of the AMNH*225 (1995).

ACKNOWLEDGMENTS

We acknowledge the traditional owners of Australia and the Meintangk, Marditjali, and Potaruwutj custodians of the Naracoorte region. We thank the hundreds of volunteers, students, and scientists who collected and prepared specimens from VFC. We are grateful to M.-A. Binnie, S. Ingleby, H. Janetzki, K. Roberts, D. Stemmer, K. Travouillon, and A. Yates for access to specimens; L. DeSantis and J. van Zoelen for providing casts; T. Prowse for modeling assistance; I. Kerr for *Protemnodon* locality data; C. McArthur, G. Merceron, P. Ungar, A. Couzens, R. Correll, and E. Shute for comments and discussion; and I. Calandra and C. Johnson for helpful reviews. **Funding:** This work was funded by Australian Research Council grants (DP110100726, FT130101728, LE130100115, DP190103636 to G.J.P.) S.D.A. and G.A.G. were supported by Flinders University Research Scholarships. **Author contributions:** S.D.A. and G.J.P. designed the study and wrote the paper; S.D.A. collected and analyzed data; G.A.G. contributed to analytical design and wrote the paper. **Competing interests:** The authors declare no competing interests. **Data and materials availability:** Data files for analyses are available in the supplementary materials and the dryad archive associated with the article (*38*).

SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.adq4340
Materials and Methods
Supplementary Text
Figs. S1 to S17
Tables S1 to S6
References (*43*–*75*)
MDAR Reproducibility Checklist
Data S1 and S2

Submitted 23 May 2024; accepted 27 November 2024
10.1126/science.adq4340

Correction (17 March 2025): An extended version of Fig. 3 was erroneously used; both the figure and the legend have been corrected and the figure now only contains the first panel instead of panels A to E.